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The Status and Affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto

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INTRODUCTION

Hyaena sinensis was described by Owen (1870) on the basis of fragmentary material (one P⁸, and one P₃, and a broken canine) from a cave near Chungking in the province of Szechwan, China. *Hyaena ultima* was based by Matsumoto (1915) on even more scanty material (one P⁴) from "a certain marly district of Szechuan, China." Both species occurred associated with a similar fauna, correlative with that of the *Sinanthropus* site at Choukoutien, and characterized by the presence of *Stegodon orientalis* Owen. A third contemporary species, *Hyaena zdanskyi*, was described by Pei (1934a) from Choukoutien.

The two first-mentioned species have been recorded from several localities. Thus Koken (1885) attributed a collection of teeth, probably from Yunnan, to Owen's species. Zdansky (1925, 1927, 1928) recorded *H. sinensis* from Choukoutien, near Peking, and from Yüanchü (province of Shansi), and *H. ultima* from Hsin-an-hsien (province of Honan). Pei (1934a) described abundant material of *H. sinensis* and a single jaw of *H. ultima* from the *Sinanthropus* site of Choukoutien. *Hyaena sinensis* has also been reported from Chingshihling (near the border of the provinces of Hopei and Shansi) by Young and Pei (1933). *Hyaena ultima* has been found at many localities, including the Choukoutien Upper Cave (Pei, 1934b); Hoshangtung, Yunnan (Bien and Chia,

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1938); Kweilin, Kwangsi (Pei, 1935); Tanyang, Kiangsu (Pei, 1940); Tam nang, Indochina (Arambourg and Fromaget, 1938); Harbin, Manchuria (Tokunaga and Naora, 1939); and Dokantin, Korea (Tokunaga and Mori, 1939).

Colbert and Hooijer (1953) described excellent skull and jaw material of a large hyena, identifiable with *H. ultima* Matsumoto, from fissure fillings near Yenchingkou in the province of Szechwan. These authors, however, identified their material with Owen's species, and reached the following conclusions: (1) that Matsumoto's and Owen's material belongs to a single species; (2) that this species is a large extinct subspecies of the spotted hyena and should be known as *Crocuta crocuta sinensis*; and (3) that all the middle Pleistocene hyenas from these sites are likely to belong to that subspecies, though a note of caution is given for the material from Yunnan, Honan, and Choukoutien. They also emphasized that *H. zdanskyi* Pei does not differ specifically from the main form at Choukoutien.

I have recently had the opportunity to study several important collections of Pleistocene Hyaenidae from China, Java, India, and Europe. While agreeing that the Yenchingkou hyena (together with other forms classified as *H. ultima*) represents a subspecies of *Crocuta crocuta*, and that *H. zdanskyi* is identical with *H. sinensis*, I am convinced that *H. ultima* and *H. sinensis* are distinct and were correctly identified by Koken, Zdansky, and Pei. I also propose to show that *H. sinensis* does not belong to the genus *Crocuta* at all, but is a true *Hyaena*—a conclusion which may, perhaps, also be read into Pei's (1934a, p. 117) statement that the "*Crocuta* type . . . differs at first glance from any representative of the *sinensis* group."

During the study of the affinities of *H. sinensis* it became clear that a number of other hyaenids belonging to *Hyaena* have been incorrectly assigned to the genus *Crocuta*. The usual criterion, as formulated by Pilgrim (1931, p. 115), has been the presence or absence of a distinct metaconid in M_1 . It is now clear that this character is totally unreliable, and that such forms as *Hyaena perrieri* Croizet and Jobert, *Hyaena brevirostris* Aymard, *Hyaena bathygnatha* Dubois, and probably *Hyaena salonicae* Andrews are representatives of the genus *Hyaena*. The interrelationships of these forms and the descent and subspeciation of *Crocuta crocuta* are discussed below. Apart from their evolutionary interest, the results have a bearing on Pleistocene stratigraphy in furnishing a new and unexpected fixed point for the correlation of a number of important faunas.

MATERIAL AND METHODS

The following samples have been personally examined:

Recent *Crocuta crocata* (about 170 skulls), *Hyaena hyaena* (about 70 skulls) and *Hyaena brunnea* (15 skulls), mainly in the Zoological Department of the British Museum (Natural History). The spotted hyena collection includes a large homogeneous sample from Balbal in Tanganyika Territory (the L. Harrison Matthews collection).

Crocuta crocata ultima, specimens in the Lagrelius collection, Uppsala, and a cast of the dentition of a specimen in the American Museum of Natural History.

Crocuta crocata spelaea, large samples in the Krahuletz Museum of Eggenburg, Austria, in the Paleontological Institute of Vienna University, and in the Geological Department of the British Museum (Natural History).

Hyaena sinensis, specimens in the Lagrelius collection, and in the von Koenigswald collection, Utrecht, and the type collection in the British Museum (Natural History).

Hyaena bathygnatha, specimens in the Dubois collection, Leiden, and in the von Koenigswald collection.

Hyaena brevirostris, *Hyaena perrieri*, and various other forms, including the collection of Siwalik Hyaenidae, in the British Museum (Natural History).

Smaller collections of various Hyaenidae have been examined in the Castle Museum, Norwich (Forest Bed material), the natural history museums of Vienna, Mainz, and Wiesbaden, and the Geological Institute of Helsingfors University.

Furthermore, a number of quantitative data have been obtained from the literature. Often the pertinent data are not given, or, if they are, the method of mensuration is not clearly specified. Mostly the method of mensuration is self-evident, or, if not, the individual variation in method has little effect; but in some cases the bias may be important. Thus the length of the talonid in M_1 may be measured in several ways, and the resulting figures may differ much from one another. This dimension appears to be too badly delimited for use in statistical work, and I have chosen the trigonid length instead, from the foremost point of the anterior cingulum to the hind border of the protoconid.

Wherever possible the published data have been checked by mensuration directly from figures; moreover, for a number of quantitative data, I have been forced to rely exclusively on measurements obtained in this

way. This procedure poses some quite special problems. In the first place, old works are sometimes unreliable as to exact proportions. Even if it be granted that the figure is correct, the scale may not be accurately given, or the perspective may influence the relative dimensions. The former source of bias may often be eliminated by a comparison of published measurements of some dimension (e.g., skull length or crown length of a tooth) with the figure, and the use of the correction factor thus obtained. The second source of bias is more intricate, but it may be to some extent avoided if several figures of the same object from different angles are published. Every mensuration from figures has been most painstakingly checked by these methods. In some cases it has been possible to check the data by subsequent mensuration of the specimen itself; the bias, it turned out, was too slight to influence the problem under study. Some similar checks in a collateral study of bears have confirmed this conclusion. When such data are interpreted, of course, the method of sampling should be kept in mind; data of this sort have different validity for different kinds of problems.

Quantitative data of one sort or another have been culled from the following sources: Bien and Chia (1938), Boule (1893), Boule and Teilhard (1928), Colbert (1935, 1939), Colbert and Hooijer (1953), Ehrenberg (1938-1940), Ewer (1954b), Geib (1915), Koken (1885), Matsumoto (1915), Pei (1934a), Pilgrim (1932), von Reichenau (1906), Soergel (1936, 1937), Teilhard and Piveteau (1930), Viret (1954), and Weithofer (1889).

The statistical handling of the data does not, in general, go beyond the standard procedures described in Simpson and Roe (1939), but I have also made use of the ratio diagram method of Simpson (1941) for comparing average proportions of samples, and of the methods for study of allometry in mammalian teeth described in Kurtén (1954a).

For permission to study the collections in their care, and for numerous courtesies extended to me, I am much indebted to Mr. N. W. Edwards, London; Mr. E. Ellis, Norwich; Mr. R. W. Hayman, London; Dr. Dirk A. Hooijer, Leiden; Dr. Olavi Kalela, Helsingfors; Prof. G. H. R. von Koenigswald, Utrecht; Messrs. F. Schäffer and J. Hamböck, Eggenburg; Drs. Erich Thenius and Helmuth Zapfe, Vienna; Prof. Per Thorslund, Uppsala; and the staffs of the natural history museums of Wiesbaden and Mainz. I also wish to acknowledge gratefully the bibliographic help received from Dr. Birger Bohlin, Uppsala; Dr. Edwin H. Colbert, New York; and Mrs. Rachel H. Nichols, New York. To Dr. Colbert, again, my gratitude is due for kind cooperation in exchange of

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The following abbreviations are used:

A.M.N.H., the American Museum of Natural History

B.M., the British Museum (Natural History)

G.S.I., the Geological Survey of India

THE IDENTIFICATION OF *HYAENA SINENSIS*

The disagreement on the status of *Hyaena sinensis* and *H. ultima* arose from the fact that the former species was based on material which has been considered indeterminate (e.g., by Pei, 1934a), whereas there can be no doubt that the type carnassial of *H. ultima* represents a *Crocuta*. Colbert and Hooijer (1953, p. 66) remark, "A priori, since Koken's specimens came from a locality far removed from that for the type, while Matsumoto's specimen came from some place reasonably close to the type locality, one might be justified in supposing that it would be Matsumoto's specimen that could be identified with Owen's type, not Koken's." The same argument is implied to be valid for the Yenchingkou hyena, which is from Szechwan, as are the two types. It is, moreover, reënforced by the fact that some other species from Yenchingkou may be identified with Owen's types (*Stegodon orientalis*, *Rhinoceros sinensis*, *Nestoritherium sinense*).

The argument, however, loses most of its force when it is considered that two different hyenas do occur at Choukoutien (which is amply demonstrated below), and that the fossils in the three collections (Owen's, Matsumoto's, and the Yenchingkou sample) evidently came from quite different caves. Furthermore, the situation at Choukoutien, with a large *Hyaena* and a *Crocuta crocuta* present, is repeated at some other localities, as is shown below. We are forced back to morphologic study of the type specimens themselves.

Of the type collection of *Hyaena sinensis* Owen, the broken canine is much too small to belong with the other teeth; moreover, it is quite certainly not the canine of a hyaenid at all. The lower border of the enamel, which is clearly visible, is much more oblique than in any hyena, and the cross section of the tooth is more elongate. The specimen may have belonged to a small bear, for instance, *Ursus thibetanus* G. Cuvier (= *U. kokeni* Matthew and Granger).

The premolars are only very slightly worn and are well preserved.

They are identifiable without the slightest doubt, and they are not the premolars of *Crocuta c. ultima*. Between the posterior cingulum and the main cusp of the upper third premolar there intervenes a distinct accessory cusp, an arrangement typical of *Hyaena* but never seen in *C. c. ultima* (or in any other subspecies of *C. crocuta*), where the minute posterior cusp is formed directly by the cingulum itself. This character is also seen in the lower premolar, though more weakly developed; again, it suggests *Hyaena*, not *Crocuta crocuta*. A study of these characters in referred specimens confirms the conclusion. The character is diagnostic, and the determinations of Koken, Zdansky, and Pei are correct.

Apart from this, it may be noted that Owen expressly characterized his *H. sinensis* as having unusually brachydont third premolars. On the other hand, all specimens of *C. c. ultima* known to me and showing the character have very hypsodont third upper premolars. A.M.N.H. No. 18730 from Yenchingkou (figured by Colbert and Hooijer, 1953, pls. 12-13), in fact, has the relatively highest P^3 that I have ever seen in a fossil or recent hyena—an impression that I could verify on a cast of the specimen.

All species of the genus *Hyaena* (as well as many of the genus *Crocuta*) have a more brachydont P^3 , on the average, than the recent or fossil *C. crocuta*, as shown by the scatter diagram (fig. 1). For the type of *H. sinensis* it was necessary to restore the slightly worn tip of the crown; its height cannot have exceeded 22.0 mm., as measured from the external basal incurvation. The diagram shows that the members of *Hyaena* form a very uniform series, the average hypsodonty being fairly constant in different species (see also table 1). In *C. crocuta*, the living form and *C. c. spelaea* agree in average hypsodonty, whereas the three specimens of *C. c. ultima* average somewhat more hypsodont.

An analysis of the hypsodonty indices,

$$H.I. = \frac{100 \times \text{crown height}}{\text{crown length}}$$

permits a more precise evaluation of the data. The statistics are given in table 1. The index for the type P^3 of *H. sinensis* almost certainly did not exceed 83, so it is outside the standard range of *C. crocuta*. The odds for its belonging to a spotted hyena are far less than one to a thousand.

A comparison between *C. c. ultima* and *C. c. spelaea* shows that the greater hypsodonty of the former is probably, but not certainly, significant. The difference may be tentatively regarded as a subspecific char-

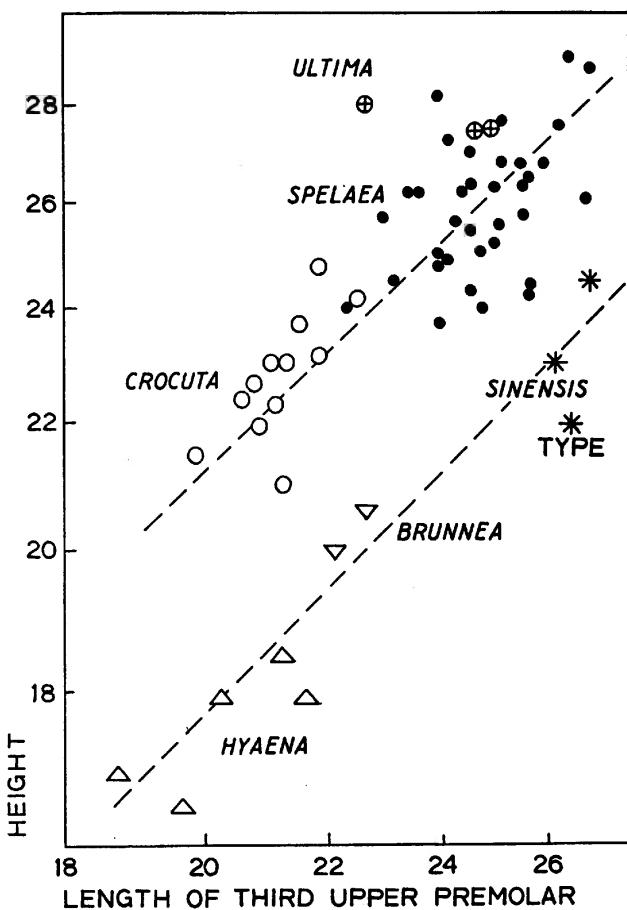


FIG. 1. Covariation of crown length and crown height (external, from basal incurvation) of unworn third upper premolars in populations of *Crocuta* and *Hyaena*, as labeled.

acter¹; at any rate, it makes it still more improbable that the type of *H. sinensis* was drawn from the *C. c. ultima* population.

On the other hand, it will be clear without further analysis that Owen's type fits excellently into the *Hyaena* series and agrees with the form here classed as *H. sinensis*.

In view of the heterogeneity of Owen's type collection it seems desirable to select a lectotype for *Hyaena sinensis* Owen. The syntype third upper premolar, B.M. No. 41937, is hereby designated lectotype.

¹ But not the only one, and not in itself decisive. Other characters are given in this paper.

The study of the type collection has proved the distinction between the two Chinese forms and has shown that their correct trivial designations are *sinensis* and *ultima*, but the generic relationships of the former are not, so far, settled. Some species of *Crocuta* have a more brachydont P^3 than *C. crocuta*, and a distinct posterior cusp may also occur in that genus. If the comparison is extended to other dental elements, however, there can be little doubt about the true position of Owen's species.

**MORPHOLOGY OF HYAENA SINENSIS AND
CROCUTA CROCUTA ULTIMA**
UPPER CARNASSIAL

In upper carnassials of equal length, the metastyle is modally much shorter in *Hyaena* than in *Crocuta*. This difference has often been noted, and indices (e.g., expressing metastyle length in per cent of crown length) are in common use. What has been overlooked is the fact that

TABLE 1
HYPSDONTY INDICES (HEIGHT IN PER CENT OF LENGTH) FOR THIRD UPPER PREMOLARS IN POPULATIONS OF *Hyaena* AND *Crocuta*

	<i>N</i> ^a	<i>M</i>	σ	<i>S. R.</i>
<i>Hyaena hyaena</i>	5	86.8±1.1	2.6±0.8	78.5-95.1
<i>Hyaena brunnea</i>	2	90.4	—	—
<i>Hyaena sinensis</i>	3	87.3	—	—
<i>Crocuta crocuta crocuta</i>	12	107.4±1.0	3.4±0.7	96.3-118.5
<i>Crocuta crocuta spelaea</i>	35	105.1±0.8	4.9±0.6	89.2-121.0
<i>Crocuta crocuta ultima</i>	3	114.7	—	—

^a *N*, number of specimens; *M*, mean; σ , standard deviation; *S. R.*, standard range (from standard deviation).

the modal relation between metastyle and crown lengths is dependent on size and suffers profound change in both genera with increasing or decreasing size. This appears clearly from the scatter diagram (fig. 2) in which metastyle length is plotted logarithmically against crown length for species of *Crocuta* and *Hyaena*: the slope of both regressions is steeper than 45 degrees. The coefficient of allometry is practically the same for both, 1.29 for *Crocuta* and 1.23 for *Hyaena*. For convenience in practical work, the modal metastyle lengths for different lengths of P^4 have been calculated in table 2, which also shows the change of the index.

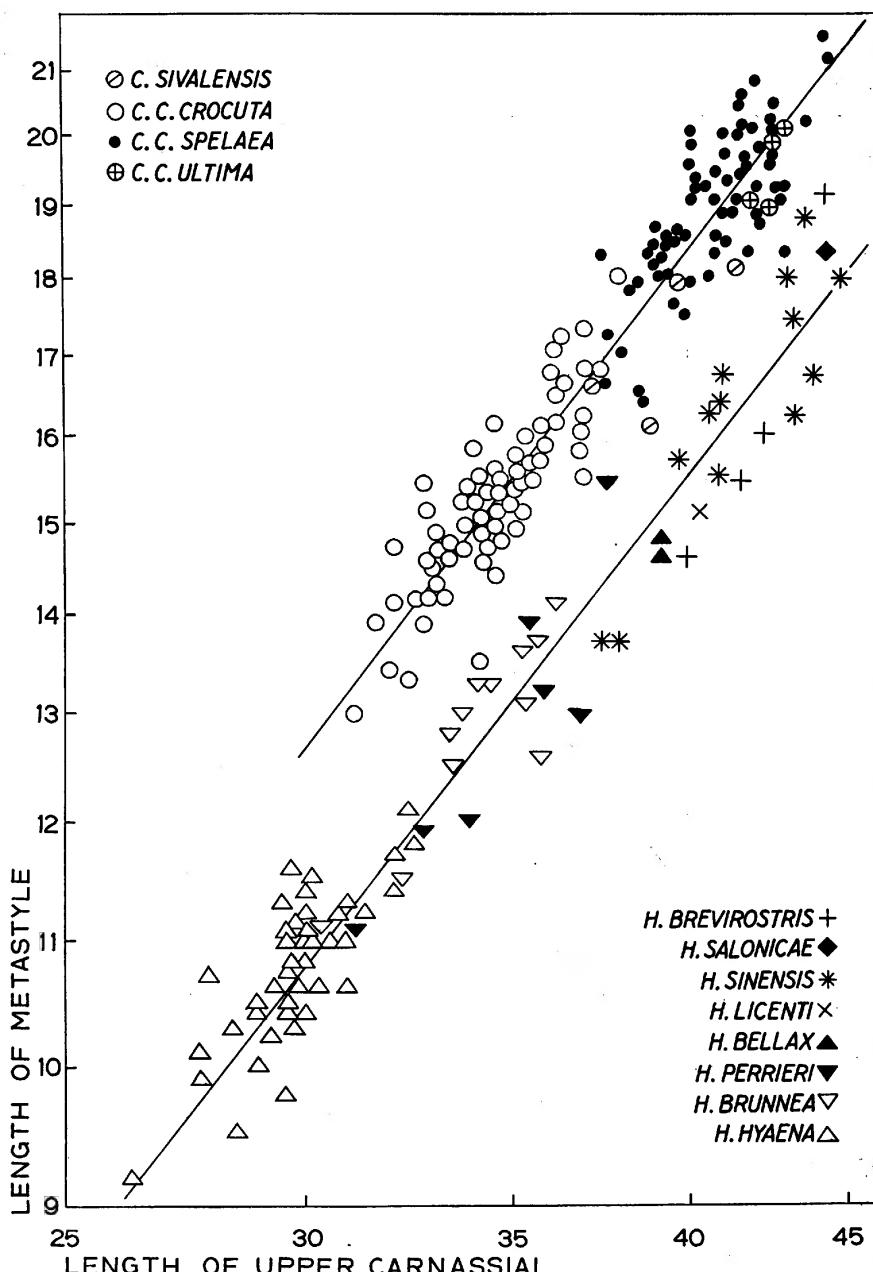


FIG. 2. Covariation of crown length and metastyle length (measured internally) of upper carnassial in populations of *Crocuta* and *Hyaena*, as labeled.

In figure 2 I have included representatives of the genus *Hyaena* and of two species of *Crocuta*, both of which belong to the group with a large protocone in P^4 . The relation has also been tested for the *Crocuta* group with a reduced protocone, and the results appear in figure 3. This third group takes an intermediate position between *Hyaena* and the *C. crocuta*-*C. sivalensis* group. It would seem useful to distinguish it by a sub-generic name. *Crocuta (Percrocuta)* Kretzoi, 1938, with the type species *Crocuta carnifex* Pilgrim, has line priority.

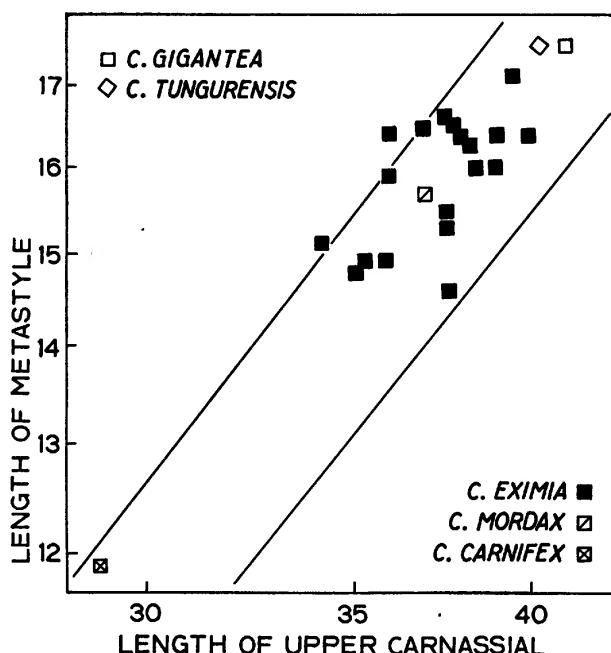


FIG. 3. Covariation of crown length and metastyle length of upper carnassial in populations of *Crocuta (Percrocuta)*, as labeled. The regression lines are those for *Crocuta (Crocuta)* and *Hyaena*, as in figure 2.

Most other Hyaenidae seem to conform to either the *Crocuta (Crocuta)* or the *Crocuta (Percrocuta)* type, except perhaps *Hyaena ("Hyaenictis") bosei* Matthew, which is likely to be a true *Hyaena*. Thus the genus *Hyaena* seems to be sharply set off from the rest of the family, or from most of it, and is readily definable.

The relative lengthening of the metastyle in large members of *Hyaena* causes the carnassial, as it were, to simulate that of a small or medium-sized *Crocuta*. Table 2 shows that the metastyle to crown length index for a very large *Hyaena* carnassial is very close to that for a small *Cro-*

cuta (*Crocuta*) carnassial, and quite different from the indices for the relatively small living species of *Hyaena*. This spurious similarity was apparently one of the reasons for placing such forms as *H. brevirostris*, *H. perrieri*, and *H. salonicae* in *Crocuta*, a procedure almost universally

TABLE 2
MODAL RELATIONS BETWEEN THE LENGTH OF THE UPPER CARNASSIAL AND
THAT OF ITS METASTYLE IN *Hyaena* AND *Crocuta (crocuta)*

Length, Carnassial	<i>Hyaena</i>		Length, Metastyle	
	Absolute	Relative	Absolute	Relative
48	19.0	40%	22.6	47%
46	18.0	39	21.4	46
44	17.0	39	20.3	46
42	16.0	38	19.1	45
40	15.1	38	17.9	45
38	14.1	37	16.8	44
36	13.2	37	15.6	43
34	12.3	36	14.5	43
32	11.4	36	13.4	42
30	10.7	36	12.3	41
28	9.9	35	11.3	40
26	9.0	34	10.5	40

adopted by paleontologists who accept the division between the genera.

There is a slight overlap between extreme variants in the two genera. Such variants, however, generally turn up in large samples only, where the determination may be based on modal characters.

Among other characters it may be noted that the parastyle is generally more prominent in *Hyaena* than in *Crocuta*, and that the protocone usually is directed obliquely forward in *Crocuta* (*Crocuta*) and laterally in *Hyaena*; finally, the blade is relatively broader in *Hyaena*.

Both in the length of the metastyle and in other characters, *H. sinensis* is a perfectly typical *Hyaena* and is easily distinguished from *C. c. ultima*. The same holds for the other forms here classed in *Hyaena*—*H. brevirostris*, *H. perrieri*, *H. licenti*, and *H. salonicae*. It should, however, be pointed out that the protocone of the last-mentioned form is somewhat reduced, and that it might represent a variant of the *Crocuta* (*Percrocuta*) stock.¹ All of these form a continuous series with the species

¹ This was the opinion of Kretzoi (1938), who placed *H. salonicae* in the new genus *Adcrocuta* together with *C. examia*, *C. gigantea*, and *C. mordax*.

usually placed in *Hyaena*, *H. hyaena*, *H. brunnea*, and *H. bellax*. The type and referred specimens of *H. zdanskyi* Pei differ from *H. sinensis* only in size, but they are within the probable range of variation of the latter and can only be considered as artificially separated extreme variants of the *sinensis* population.

Thus, among the advanced Hyaenidae, three separate groups, each apparently homogeneous, may be distinguished: *Hyaena*, with a short metastyle, a prominent protocone directed medially, a stout blade, and generally a prominent parastyle; *Crocuta* (*Crocuta*), with a long metastyle, a prominent protocone directed obliquely forward, a slender blade, and a small parastyle; and *Crocuta* (*Percrocuta*), with a metastyle of medium length and a reduced protocone. The history of *Hyaena* extends back to the lower Pliocene (if *H. salonicae* does belong here and is correctly dated); that of *Crocuta* (*Crocuta*) to the Villafranchian (or possibly to the middle Pliocene, if *C. borissiaki* Khomenko belongs here); and that of *Crocuta* (*Percrocuta*) to the upper Miocene. The last-mentioned line became extinct before the Pleistocene and is discussed only in passing; it is not likely to enter directly into the ancestry of the forms concerning us here.

LOWER CARNASSIAL

The development of the metaconid in M_1 has been used as a generic character. This procedure is invalid, as is shown here. But the lower carnassial does give important clues for the classification of the advanced Hyaenidae.

METACONID: *Crocuta* has been defined as lacking a metaconid, but it

TABLE 3
FREQUENCY OF M_1 METACONID IN POPULATIONS OF *Crocuta crocuta*

	N	Metaconid Frequency
<i>Crocuta crocuta crocuta</i>	129	17%
<i>Crocuta crocuta spelaea</i>		
Lindenthal ^a	13	100
Varia, Middle Europe ^a	21	43
Kent's Cavern	37	46
Varia, Great Britain	27	30
All except Lindenthal	85	40

* Data from Soergel.

is of course well known that even *C. crocuta* may retain this cusp occasionally. The character is quite common in some populations (table 3). In the sample from the Lindenthal Cave at Gera in Germany, described by Soergel (1937), the presence of a metaconid is normal. In other European cave hyena samples, almost one-half of the specimens possess a more or less distinct metaconid. In the living form the character is much less common. The position of the cusp is variable, and it may shift backward even to the extent of completely migrating to the talonid. In some cases, therefore, what appears to be a diminutive talonid cusp may in reality be the vestigial metaconid.

Soergel concluded that the Lindenthal cave hyena represents an earlier evolutionary stage than most other samples, an opinion which seems to be supported by stratigraphic evidence. The reduction of the metaconid in later cave hyenas and in the recent spotted hyena would, then, represent parallel trends. De Serres *et al.* (1839) erected a new species, *H. intermedia*, for a specimen from Lunel-Viel with a metaconid, but subsequent investigation by Harlé (1910) showed that the specimen was an exceptional one in a normal cave hyena sample, so that the name is not valid even subspecifically. There does not appear to be any reason for giving subspecific rank to the European populations with metaconid normally present, as the character is quite common in all cave hyena populations.

In *Crocuta c. ultima* the metaconid appears to be very frequently present, for instance in A.M.N.H. No. 18730 and in the specimen described by Zdansky (1927). It is absent from Pei's (1934a) specimen from the *Sinanthropus* site and variable in the sample from the Choukoutien Upper Cave (Pei, *ibid.*). It is present in the hyena from Sjara-Osso-Gol, as noted by Boule and Teilhard (1928). The latter was described as *C. c. spelaea* but should be placed in *C. c. ultima*.

The metaconid is also present in *C. c. piligrimina* Rao from the Karnul Caves of India—at any rate in the cast, B.M. No. M2960. It appears to be mostly or invariably present in *C. sivalensis*.

Hyaena hyaena and *H. brunnea* always have a metaconid, but in the latter it is commonly partly or wholly confluent with the protoconid. In *H. perrieri* the metaconid is usually absent, but some specimens have the cusp (see Viret, 1954); when present it is a stronger cusp than in *C. crocuta*, and reminiscent of that of *H. brunnea*. *Hyaena arvernensis* was based on such a specimen. *Hyaena brevirostris* from Europe apparently always lacks the metaconid. Of the carnassials of *H. blythogaster* that I have seen, three are without a metaconid, whereas the fourth has a vestige. Teilhard and Piveteau (1930) state that the metaconid is lacking

in *H. licenti*, but their figure shows what appears to be the outline of a vestige, in slightly raised relief on the inner wall of the protoconid; the impression may be spurious because of a crack in the enamel. In the great majority of the *H. sinensis* population the metaconid is absent, but a few specimens show the cusp. In one, figured and discussed by Pei (1934a), it is present on one side and absent on the other. When present it is of the same type as in *H. perrieri* and *H. brunnea*, not as in *C. crocata*.

It is now quite evident that there exist all sorts of transitions in both genera, and that the presence or absence of the metaconid has no value as a generic character for *Crocuta* and *Hyaena*.

TALONID: In *Crocuta* (*Crocuta*) this element is small or vestigial, with one or two more or less distinct cusps, extremely variable in development and position; a third cusp, which may appear, perhaps represents the metaconid. In *Hyaena* there exists a graded transition between the condition in *H. hyaena*, with well-developed entoconid and hypoconid,¹ to *H. sinensis*, where only the entoconid is present.² Both are present, but the hypoconid is reduced, in *H. brunnea*, *H. perrieri*, and *H. licenti*. Pei distinguished *H. licenti* from *H. sinensis* on the basis of this difference in the talonid, which gives the latter form a more progressive facies. In the type of *H. brevirostris* the talonid is bicuspid, according to Boule (1893); from the figures it appears that the hypoconid is very much reduced. In a specimen of *H. brevirostris* (*H. "robusta"*), B.M. No. M4478, from Val d' Arno, the hypoconid appears to be absent, but the tooth is rather heavily worn. Good evidence of a transition is, however, given by the four *H. bathygnatha* carnassials from the Djetis Zone of Java in von Koenigswald's collection, of which three have a unicuspid, and the fourth has a bicuspid, talonid.

RELATIVE TRIGONID LENGTH: As previously stated, the trigonid length is a more useful character for quantitative study than the length of the talonid. The relation between trigonid and crown length, expressed in the form of an index, gives of course a measurement of the amount of reduction of the talonid. The statistics for this index appear in table 4.

The mean of the index varies between 89.9 and 91.5 for the three samples of *C. crocata*. The differences between the subspecies are trifling, but a test shows that the difference in means between *C. c. crocata* (recent) and *C. c. spelaea* is valid ($d/\sigma_d = 5.53$, and P is much less than

¹ In exceptional cases the talonid may be tricuspid, as noted by Ehrenberg (1938-1940, pt. 1).

² Pei (1934a) interprets the entoconid as a hypoconid, but the transitional sequence shows the present interpretation to be more probable.

0.001); the talonid of the recent form is significantly more reduced than that of the cave hyena. The index for *C. c. ultima* is still lower than that for *C. c. spelaea*, but the sample is small, and these differences cannot be shown to be significant.

TABLE 4

LENGTH OF TRIGONID IN PER CENT OF TOTAL LENGTH OF LOWER CARNASSIAL
IN POPULATIONS OF *Hyaena* AND *Crocuta*

	<i>N</i>	<i>M</i>	σ	<i>S. R.</i>
<i>Hyaena hyaena</i>	46	80.02±0.21	1.45±0.15	75.3–84.7
<i>Hyaena brunnea</i>	12	83.49±0.66	2.29±0.47	76.1–90.9
<i>Hyaena sinensis</i>	15	83.39±0.48	1.86±0.34	77.4–89.4
<i>Hyaena perrieri</i>	6	84.70±0.57	1.38±0.40	80.2–89.2
<i>Hyaena bathygnatha</i>	4	86.57±0.72	1.43±0.51	81.8–91.3
<i>Crocuta sivalensis</i>	2	81.75	—	(81.5–82.0) ^a
<i>Crocuta crocuta ultima</i> . . .	5	89.90±0.66	1.47±0.47	85.1–94.7
<i>Crocuta crocuta spelaea</i> . . .	114	90.17±0.12	1.29±0.09	86.0–94.3
<i>Crocuta crocuta crocuta</i> . . .	53	91.46±0.18	1.28±0.12	87.3–95.6

^a Observed range.

Two specimens of *C. sivalensis* have much lower indices. Both are well outside the standard ranges for the index in the three subspecies of *C. crocuta*, and a specific separation between *C. sivalensis* and *C. crocuta* appears to be correct. The condition in the Siwaliks form is more primitive.

For two specimens of *C. ultra* from Kromdraai in South Africa the indices appear to vary between 86 and 90. This form is thus within the range of *C. crocuta* rather than within that of *C. sivalensis*. Finally, in the carnassial from the Karnul Caves, mentioned above, the talonid is as short as in other specimens of *C. crocuta*; the index is almost 94.

In all members of *Hyaena* the index is lower than in *C. crocuta*. The talonid is least reduced in the recent *H. hyaena*. For *H. brunnea* and *H. sinensis* the values are practically identical, whereas *H. perrieri* and particularly *H. bathygnatha* have more reduced talonids. A series of significance tests gives the results shown in table 5. *Hyaena hyaena* differs significantly from all others. These others form two groups, which are not, however, fully separated. *Hyaena bathygnatha* differs significantly from all except possibly *H. perrieri*; *Hyaena brunnea*, *H. sinensis*, and *H. perrieri* do not differ significantly from one another. Of *H. brevirostris* I have only a small sample. In the type the index would appear

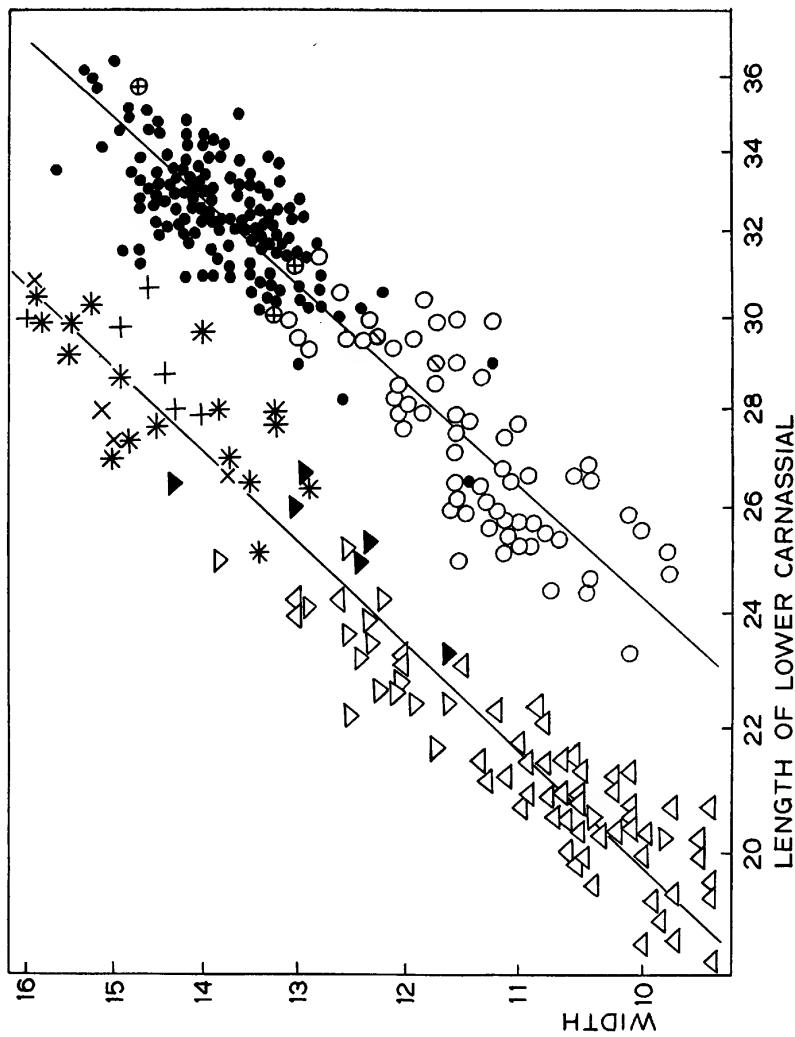


FIG. 4. Covariation of crown length and crown width (across anterior lobe) of lower carnassial in populations of *Crocuta* and *Hyena*. Symbols as in figure 2; X, *H. hyena*.

to be around 86 (agreeing with *H. bathygnatha* but within the standard range of all except *H. hyaena*) and in B.M. No. M4478 from Val d'Arno it is considerably lower, about 83.5, which is within the range of all members of *Hyaena*. The mean of these two is on the order of 84–85, as in *H. perrieri*; in a specimen from the Siwaliks, discussed below, it is about 86.

OTHER CHARACTERS: The width of M_1 is slightly positively allometric to the length in both *Hyaena* ($k = 1.07$, and all species appear to be on a single regression) and *C. crocuta* ($k = 1.10$, a single regression for all subspecies). The two regressions are roughly parallel, but not coincident; the carnassials are relatively broader in *Hyaena* (fig. 4).

In both forms the anterior lobe of M_1 is broader than the posterior one; it generally swells out more abruptly in *C. crocuta*.

TABLE 5

COMPARISON BETWEEN MEANS FOR RELATIVE TRIGONID LENGTHS OF LOWER CARNASSIALS IN SAMPLES OF *Hyaena*. TABLE OF *P* (PROBABILITY)

	<i>hyaena</i>	<i>bathygnatha</i>	<i>perrieri</i>	<i>sinensis</i>
<i>brunnea</i>	<0.001	0.005	>0.1	>0.1
<i>sinensis</i>	<0.001	0.001	0.1	
<i>perrieri</i>	<0.001	0.07		
<i>bathygnatha</i>	<0.001			

Some confusion between the lower carnassial of the large species of *Hyaena* and that of *Crocuta (Percrocuta) gigantea* (Schlosser) is possible, as they do not differ much in size, and the talonid of *C. gigantea* is bicuspid and about as much reduced as in *H. brevirostris*. It may be worth while, therefore, to point out some distinctive characters (based on a study of two specimens in Schlosser's type collection, one in the von Koenigswald collection, and B.M. No. 49998, erroneously labeled *Hyaena sinensis*).¹ Besides being generally somewhat larger, the *C. gigantea* molar is distinguished by the fact that both anterior and posterior lobes are approximately equally broad, and by the great height of the crown.

In all the characters here discussed, *C. c. ultima* and *H. sinensis* are different; on the other hand, *H. zdanskyi* agrees with *H. sinensis*.

¹ B. M. No. 49998, collected by H. N. Moseley, 1879, comes from an unknown cave deposit in China, and is labeled as of Pleistocene age. That date is probably too late, but at any rate it suggests that the species is later than the Pontian, to which it has been tentatively assigned (on not very convincing grounds) by various authors.

THE CHEEK DENTITION AS A WHOLE

A study of the relative dimensions of the elements in the cheek dentition corroborates the conclusions. Figures 5 and 6 summarize data for various hyaenid samples, treated by means of the ratio-diagram method. As a standard I have used the mean dimensions for a homogeneous sample of recent *Crocuta c. crocuta* from Balbal in Tanganyika Territory. The measurements used are the crown lengths of P^2-P^4 , M_1-P_2 , and the lower canines. The statistics appear in table 6. Figure 5 shows the data for two different samples of *C. c. spelaea* from the European Pleistocene (one from Kent's Cavern near Torquay in south England,

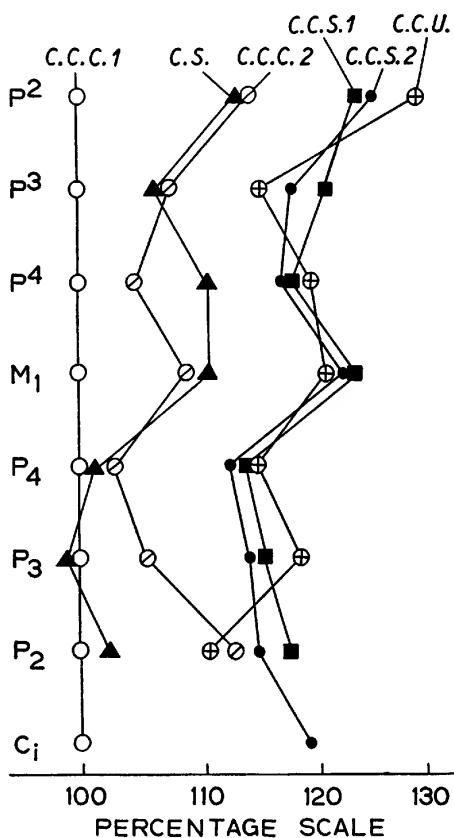


FIG. 5. Ratio diagram, comparing mean lengths of tooth crowns in samples of *Crocuta crocuta* and *C. sivalensis*. Abbreviations: C.c.c.1, *Crocuta c. crocuta*, recent, Balbal; C.c.c.2, *Crocuta c. crocuta*, recent, South Africa; C.c.s.1, *Crocuta c. spelaea*, Eggenburg; C.c.s.2, *Crocuta c. spelaea*, Kent's Cavern; C.c.u., *Crocuta c. ultima*; C.s., *Crocuta sivalensis*.

the other from the Teufelslücken Cave at Eggenburg in Austria); a sample of the living *C. c. crocuta* from South Africa; a sample of *C. c. ultima* from China and Mongolia; and a sample of *C. sivalensis* from the Siwaliks. Figure 6 shows means for *H. hyaena*, a sample from India; *H. brunnea*; *H. perrieri*, Viret's sample from Saint-Vallier in south France; *H. sinensis*, from Choukoutien and correlative strata in China; *H. bathygnatha*, from the Djetis of Java; and *H. "robusta"* (= *H. brevirostris*), according to Soergel (1937) and Weithofer (1889) from Val d'Arno in Tuscany, Italy; and the dimensions of two single specimens—the types of *H. salonicae* (from Salonica, Greece) and *H. brevirostris* (from Sainzelles, France).

Within *C. crocuta*, and between that species and *C. sivalensis*, the variation is relatively slight. The different forms deviate in absolute size, but the patterns are roughly identical. *Crocuta c. ultima* and the two samples of *C. c. spelaea* form a fairly homogeneous group. The two latter, in particular, agree almost perfectly with each other, the hyena from Eggenburg averaging very slightly larger than that from Kent's Cavern. Most of the means in *C. sivalensis* are closely approximated by one or the other of the two recent populations.

Figure 6 presents a striking contrast. The pattern is here entirely different, but all the samples placed in *Hyaena* show essential agreement with one another in their relative dimensions.

These forms differ from *Crocuta* in the relative shortness of the carnassials, particularly M_1 , and the relatively greater length of the anterior premolars, particularly P^2 . The larger forms, moreover, differ in their very large canines, but this is a trend which is initiated even in *H. hyaena*, and there is a gradual transition from the condition in that species to the extreme type of *H. brevirostris*.

The large size of the canine is reflected in the development of the lower jaw, which tapers less forward in all members of *Hyaena* than in *C. crocuta*. The relatively greater depth of the symphyseal portion serves, of course, to accommodate the root of the canine. As the canine is more vertically implanted in advanced Hyaenidae than in many other carnivores, even small differences in canine size will be reflected in the shape of the jaw.

The anterior premolars in *Hyaena* have other distinctive features apart from their relatively greater size. The third premolars are discussed above. The second premolars, both upper and lower, are rather low-crowned in *Crocuta* (*Crocuta*) and have a well-developed posterior cusp, sharply set off from the main cusp. In *Hyaena* they are more hypodont, and the posterior cusp is weaker. The lower canines of

Hyaena have a somewhat more elongate cross section than those of *Crocuta* (*Crocuta*).

The first upper molar is broad and tritubercular in all species of *Hyaena*. In *C. crocata* the tooth is either absent or a small peg-like struc-

TABLE 6
LENGTHS OF TOOTH CROWNS IN POPULATIONS OF *Hyaena* AND *Crocuta*

		N	M	σ	V ^a	S. R.
<i>Hyaena hyaena</i> India	P ²	38	16.36±0.12	0.77±0.09	4.68±0.54	13.9-18.8
	P ³	37	20.83±0.10	0.59±0.07	2.82±0.33	18.9-22.7
	P ⁴	39	30.01±0.12	0.76±0.09	2.52±0.29	27.6-32.5
	M ₁	37	20.78±0.10	0.60±0.07	2.88±0.34	18.8-22.7
	P ₄	38	20.46±0.09	0.55±0.06	2.68±0.31	18.7-22.2
	P ₃	37	19.24±0.08	0.47±0.05	2.46±0.29	17.7-20.8
	P ₂	37	14.24±0.10	0.60±0.07	4.21±0.49	12.3-16.2
	C _i	6	14.52±0.27	0.65±0.19	4.48±1.29	12.4-16.6
<i>Hyaena brunnea</i>	P ²	18	17.23±0.16	0.69±0.12	4.02±0.67	15.0-19.5
	P ³	18	22.62±0.22	0.94±0.16	4.18±0.70	19.6-25.7
	P ⁴	18	34.56±0.36	1.53±0.25	4.42±0.74	29.6-39.5
	M ₁	20	23.21±0.25	1.10±0.17	4.76±0.75	19.6-26.8
	P ₄	20	22.73±0.18	0.78±0.12	3.45±0.55	20.2-25.3
	P ₃	19	20.26±0.17	0.72±0.12	3.56±0.58	17.8-22.6
	P ₂	18	15.04±0.12	0.53±0.09	3.51±0.59	13.3-16.8
	C _i	10	16.95±0.26	0.82±0.18	4.81±1.08	14.3-19.6
<i>Hyaena perrieri</i> Saint-Vallier	P ²	3	18.23±0.50	0.87±0.36	4.80±1.96	15.4-21.1
	P ³	3	23.73±0.86	1.50±0.61	6.31±2.58	18.9-28.6
	P ⁴	3	35.40±1.18	2.05±0.84	5.78±2.36	28.8-42.0
	M ₁	4	24.67±0.61	1.22±0.43	4.93±1.74	20.7-28.6
	P ₄	3	22.27±0.71	1.24±0.51	5.55±2.27	18.3-26.3
	P ₃	3	20.23±0.31	0.54±0.22	2.69±1.10	18.5-22.0
	P ₂	3	15.60±0.45	0.79±0.32	5.05±2.06	13.1-18.1
	C _i	1	17.7			
<i>Hyaena sinensis</i>	P ²	7	19.96±0.41	1.10±0.29	5.49±1.47	16.4-23.5
	P ³	10	26.42±0.44	1.39±0.31	5.27±1.18	20.9-30.9
	P ⁴	12	42.06±0.58	2.01±0.41	4.78±0.97	35.6-47.6
	M ₁	17	28.05±0.34	1.39±0.24	4.94±0.85	23.6-32.5
	P ₄	14	26.27±0.37	1.39±0.26	5.29±1.00	21.8-30.8
	P ₃	15	23.78±0.32	1.25±0.23	5.27±0.96	19.7-27.8
	P ₂	10	17.94±0.37	1.16±0.26	6.47±1.45	14.2-21.7
	C _i	2	22.65			

* Coefficient of variation.

TABLE 6—(continued)

		<i>N</i>	<i>M</i>	σ	<i>V</i>	<i>S. R.</i>
<i>Hyaena bathygnatha</i>	M ₁	4	28.25±0.93	1.86±0.66	6.60±2.33	22.2–34.3
	P ₄	6	25.65±0.61	1.50±0.43	5.84±1.69	20.8–30.5
	P ₃	8	23.04±0.22	0.63±0.16	2.72±0.68	21.0–25.1
	P ₂	3	18.17±0.50	0.87±0.36	4.81±1.96	15.3–21.0
<i>Hyaena brevirostris</i> Val d'Arno	P ²	3	21.67±0.27	0.47±0.19	2.18±0.89	20.1–23.2
	P ³	4	27.50±0.25	0.50±0.18	1.82±0.64	25.9–43.8
	P ⁴	4	40.88±0.45	0.89±0.32	2.19±0.77	38.0–43.8
	M ₁	5	29.50±0.63	1.41±0.45	4.80±1.52	24.9–34.1
	P ₄	5	25.48±0.19	0.43±0.14	1.68±0.53	24.1–26.9
	P ₃	4	23.50±0.66	1.32±0.47	5.63±1.99	19.2–27.8
	P ₂	4	18.62±0.28	0.48±0.20	2.58±1.05	17.1–20.2
	C _i					
<i>Crocuta crocuta</i> <i>crocuta</i> Balbal	P ²	97	14.38±0.08	0.83±0.06	5.78±0.42	11.7–17.1
	P ³	97	21.11±0.09	0.91±0.07	4.33±0.31	18.2–24.1
	P ⁴	97	34.97±0.16	1.61±0.12	4.61±0.33	29.7–40.2
	M ₁	95	26.67±0.13	1.26±0.09	4.71±0.34	22.6–30.7
	P ₄	91	21.66±0.09	0.87±0.06	4.00±0.30	18.8–24.5
	P ₃	98	19.86±0.09	0.86±0.06	4.31±0.31	17.1–22.6
	P ₂	96	14.49±0.08	0.83±0.06	5.73±0.41	11.8–17.2
	C _i	7	14.47±0.21	0.55±0.15	3.82±1.02	12.6–16.3
	C _i					
	C _i					
<i>Crocuta crocuta</i> <i> spelaea</i> Kent's Cavern	P ²	18	17.97±0.23	0.96±0.16	5.35±0.89	14.9–21.1
	P ³	37	24.81±0.21	1.25±0.15	5.04±0.59	20.8–28.9
	P ⁴	39	40.83±0.20	1.28±0.14	3.14±0.36	36.7–45.0
	M ₁	41	32.61±0.18	1.14±0.13	3.48±0.38	28.9–36.3
	P ₄	52	24.28±0.15	1.07±0.10	4.40±0.43	20.8–27.7
	P ₃	53	22.61±0.13	0.98±0.10	4.33±0.42	19.4–25.8
	P ₂	45	16.56±0.10	0.70±0.07	4.22±0.45	14.3–18.8
	C _i	18	16.64±0.23	0.97±0.16	5.84±1.04	13.5–19.8
	C _i					
	C _i					
<i>Crocuta crocuta</i> <i> ultima</i>	P ²	4	18.48±0.42	0.85±0.30	4.59±1.62	15.7–21.2
	P ³	5	24.22±0.39	0.88±0.28	3.63±1.15	21.4–27.1
	P ⁴	5	41.80±0.64	1.42±0.45	3.40±1.08	37.2–46.4
	M ₁	6	32.78±0.82	2.01±0.58	6.12±1.77	27.3–39.3
	P ₄	6	24.60±0.28	0.69±0.20	2.81±0.82	22.4–26.8
	P ₃	6	23.33±0.53	1.29±0.37	5.51±1.59	19.2–27.5
	P ₂	1	16.0			
<i>Crocuta sivalensis</i>	P ²	3	16.23±0.51	0.88±0.36	5.43±2.22	13.4–19.1
	P ³	7	22.34±0.37	0.97±0.26	4.34±1.16	19.2–25.5
	P ⁴	7	38.51±0.73	1.92±0.51	4.98±1.33	32.3–44.7
	M ₁	2	29.35			
	P ₄	4	21.92±0.21	0.43±0.15	1.95±0.69	20.5–23.3
	P ₃	4	19.70±0.28	0.56±0.20	2.95±1.01	17.9–21.5
	P ₂	3	14.83±0.37	0.64±0.26	4.29±1.75	12.8–16.9

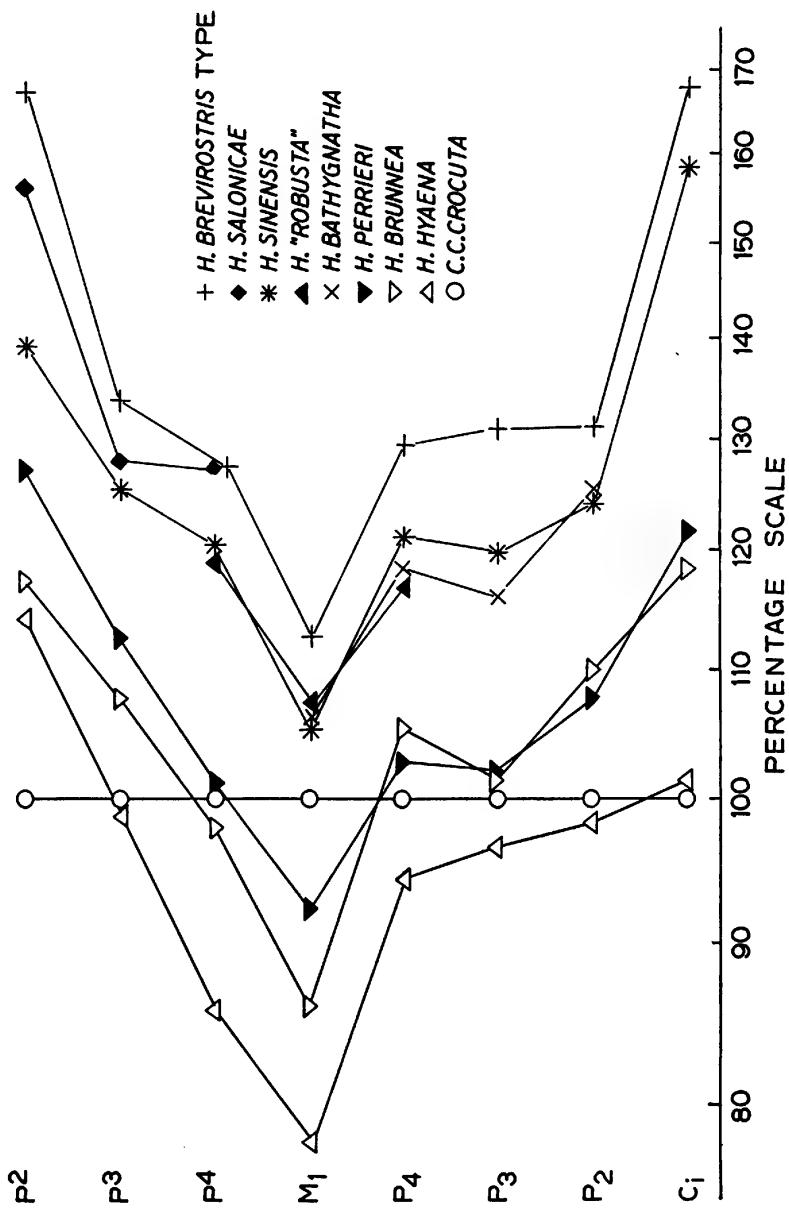


FIG. 6. Ratio diagram, comparing mean lengths of tooth crowns in samples of *Hyaena*, as labeled. Standard (100%), *Crocuta c. crocuta*, Balbal.

ture. In *C. c. spelaea* the tooth is usually absent. In *C. c. ultima* it appears to be modally slightly larger, or the mode is higher in relation to the phenotypic realization threshold,¹ judging from the width (5.4 mm.) in the specimen from locality 100, described by Zdansky (1925), but it may also be absent, as in A.M.N.H. No. 18730. In large samples of *C. c. spelaea*, exceptional specimens almost 5 mm. in width may be found. The tooth is also relatively large in *C. c. ultra* from Kromdraai. The M^1 of *C. sivalensis* averaged somewhat larger still. Even the largest specimens of *C. crocuta* are, however, so far outside the standard range of variation in *H. sinensis* (10.9–19.0 mm.) that confusion is impossible.

The variation in size of this molar in *H. sinensis* is of the magnitude to be expected in a subvestigial tooth, the coefficient of variation being of the same order as in other hyaenid populations (table 7). The tooth shows no certainly distinctive features in the specimens classed by Pei (1934a) as *H. zdanskyi*. Its size, stated by Pei to be remarkably large in the latter form, is exceeded by specimens classed by Pei as *H. sinensis*.

MILK DENTITION

The milk dentition gives particularly important information on phyletic relationships because of its well-known tendency to conservatism, a trait recently illustrated in a striking way by Crusafont and Truyols (1953). The present study is limited to the lower cheek teeth, which are most often found.

TABLE 7
WIDTHS OF FIRST UPPER MOLAR IN POPULATIONS OF *Hyaena* AND *Crocuta*

	<i>N</i>	<i>M</i>	σ	<i>V</i>	S. R.
<i>Hyaena hyaena</i> , India	40	13.54 ± 0.12	0.75 ± 0.08	5.52 ± 0.62	11.1–16.0
<i>Hyaena brunnea</i>	12	12.35 ± 0.19	0.65 ± 0.13	5.26 ± 1.07	10.2–14.5
<i>Hyaena sinensis</i>	27	14.96 ± 0.24	1.25 ± 0.17	8.36 ± 1.14	10.9–19.0
<i>Crocuta eximia variabilis</i>	14	14.70 ± 0.37	1.38 ± 0.26	9.36 ± 1.77	10.2–19.2

The deciduous lower cheek teeth are known in the recent forms and in *H. sinensis*, *H. perrieri*, *C. c. spelaea*, and *C. c. ultima*. A lower milk carnassial at one time believed to represent *H. bathynathus* was shown by Brongersma (1937) to be the D_4 of a tiger. Curiously enough, the error has been repeated at least twice. Teilhard and Piveteau (1930)

¹ For a discussion of an analogous case, see Kurtén (1953, p. 53).

attributed the milk molar of a felid to their *Hyaena* sp. from Nihowan, and Pei (1934a) figured another felid milk carnassial as belonging to *H. zdanskyi*.

Besides my own data on hyaenid milk teeth I have relied on the careful description by Ehrenberg (1938–1940, pt. 1). The milk dentitions of *H. sinensis* and *H. perrieri* have been figured by Pei (1934a) and Viret (1954), respectively. Milk teeth of *C. c. ultima* are figured by Colbert and Hooijer (1953). The data on *C. c. spelaea* pertain to the Eggenburg sample. Finally, these samples are compared with the milk teeth of *C. eximia* as a representative of the *Crocuta* (*Percrocuta*) group, based on material in the British Museum (Natural History).

The statistics are given in table 8, and the mean lengths of the milk teeth are compared in a ratio diagram (fig. 7).

The proportions in *Crocuta* and *Hyaena* are still more strikingly different than in the permanent dentition, a fact that appears to testify to ancient divergence and subsequent parallel or convergent evolution. The reduction of the anterior teeth in *C. crocuta*, as compared to *Hyaena*, shows a uniform gradient; D_2 is very much reduced, D_3 less strongly so, and D_4 is of the same order of magnitude in both. The Pontian *C. eximia* is of a somewhat intermediate type, but it is closer to *C. crocuta* than to *Hyaena*. Between the subspecies of *C. crocuta* there are no such

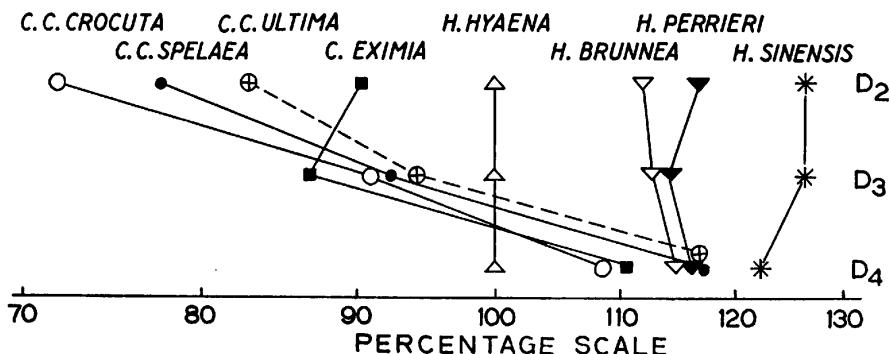


FIG. 7. Ratio diagram, comparing mean lengths of lower milk teeth in samples of *Crocuta* and *Hyaena*, as labeled.

systematic differences, and such irregularities as occur may even be caused by small-sample effects.

The patterns in the four populations of *Hyaena* are perfectly similar to one another, the only distinctive feature being gross size. Even this character does not hold for *H. perrieri* and *H. brunnea*, which are virtually identical in the dimensions of their milk teeth.

Morphological examination bears out the results. The greatly reduced D_2 of *C. crocuta* has lost almost all traces of accessory cusps. In *H. hyaena*, both anterior and posterior cusps are present; in *H. brunnea*, they are weaker; in *H. perrieri* and *H. sinensis*, the anterior cusp is reduced, but the posterior one remains prominent, uniting with the cingulum in the latter species, but not in the former. In *C. eximia* the anterior cusp is absent, and the posterior is "kaum sichtbar" (Zdansky, 1924, p. 102). D_3 is somewhat less distinctive, except for size. The tal-

TABLE 8
LENGTHS OF DECIDUOUS LOWER CHEEK TEETH IN POPULATIONS OF *Crocuta*
AND *Hyaena*

		N	M	σ	V	S. R.
<i>Crocuta crocuta</i>	D_2	4	8.62 ± 0.20	0.39 ± 0.14	4.54 ± 1.60	7.3- 9.9
	D_3	4	13.48 ± 0.08	0.17 ± 0.06	1.33 ± 0.47	12.9-14.0
	D_4	4	17.85 ± 0.62	1.23 ± 0.44	6.90 ± 2.44	13.8-21.9
<i>Crocuta crocuta</i> <i> spelaea</i>	D_2	10	9.19 ± 0.17	0.53 ± 0.12	5.76 ± 1.29	7.5-10.9
	D_3	11	13.74 ± 0.15	0.50 ± 0.11	3.64 ± 0.78	12.1-15.4
	D_4	34	19.91 ± 0.18	1.05 ± 0.13	5.30 ± 0.64	16.5-23.3
<i>Crocuta crocuta</i> <i>ultima</i>	D_2	1	10.2	—	—	—
	D_3	1	14.1	—	—	—
	D_4	1	20.0	—	—	—
<i>Hyaena hyaena</i>	D_2	9	11.76 ± 0.18	0.54 ± 0.13	4.61 ± 1.09	10.0-13.5
	D_3	9	14.86 ± 0.21	0.63 ± 0.15	4.24 ± 1.00	12.8-16.9
	D_4	8	17.09 ± 0.23	0.66 ± 0.16	3.84 ± 0.96	15.0-19.2
<i>Hyaena brunnea</i>	D_2	2	13.25	—	—	—
	D_3	2	16.75	—	—	—
	D_4	2	19.5	—	—	—
<i>Hyaena perrieri</i>	D_2	4	13.80 ± 0.39	0.78 ± 0.28	5.69 ± 2.01	11.3-16.3
	D_3	4	16.90 ± 0.35	0.70 ± 0.25	4.14 ± 1.46	14.6-19.2
	D_4	5	19.84 ± 0.53	1.18 ± 0.37	5.94 ± 1.88	16.0-23.7
<i>Hyaena sinensis</i>	D_2	5	14.96 ± 0.43	0.97 ± 0.31	6.48 ± 2.05	11.8-18.1
	D_3	7	18.73 ± 0.22	0.59 ± 0.16	3.15 ± 0.84	16.8-20.6
	D_4	7	20.82 ± 0.23	0.60 ± 0.16	2.88 ± 0.77	18.9-22.8
<i>Crocuta eximia</i>	D_2	2	10.7	—	—	—
	D_3	2	12.9	—	—	—
	D_4	1	18.5	—	—	—

onid of D_4 is characterized, in *Hyaena*, by the strong development of the entoconid. The hypoconid, in contrast, is progressively reduced in the larger forms, the trend being similar to that in M_1 ; it is absent in the milk carnassial of *H. sinensis*. In *C. crocuta* there is none of this. Both cusps are absent or have shifted to the posterior border of the tooth, for

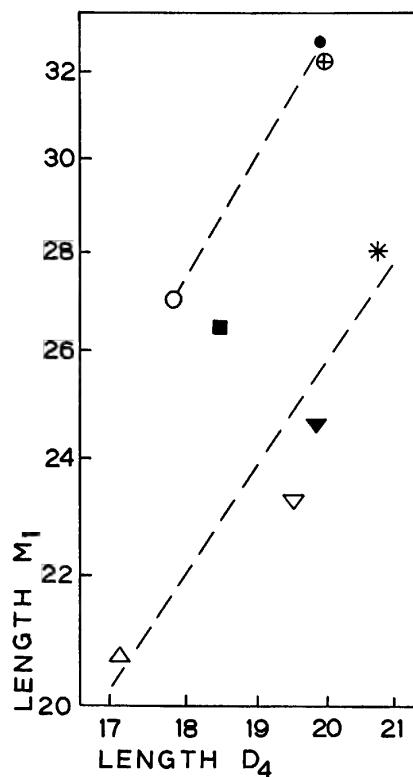


FIG. 8. Covariation of the lengths of lower milk carnassial and lower permanent carnassial in samples of *Hyaena* and *Crocuta* (means or single specimens). Symbols as in figures 2 and 3.

the talonid rises "nach hinten bald ziemlich steil bis fast senkrecht an, bald erhebt es sich nur wenig und sehr schräge zum Hinterende des Zahnes" (Ehrenberg, 1938-1940, pt. 1, p. 88), where a varying number of small cuspules or serrations are present. A different type is apparently represented by *C. eximia*, where the talonid is indistinctly tricuspid, but its summit has shifted farther back than in *Hyaena*.

A most interesting feature is observed if the lengths of the milk teeth and the succeeding permanent teeth are compared; the difference is much greater in *Crocuta* than in *Hyaena*. In figure 8 the lengths of M_1 are plotted against those of D_4 (means or single specimens). The difference, moreover, tends to be greater in larger forms, and there is thus a suggestion that M_1 actually is positively allometric to D_4 . Unfortunately, my data do not suffice to show whether this allometry also holds within populations, and not only between them. The deviations in *Hyaena* are considerable, but it should be noted that the D_4 sample for *H. brunnea* is very small and that for *H. perrieri* heterogeneous (four specimens from Saint-Vallier, one from Mt. Perrier). The three subspecies of *C. crocuta* seem to form one homogeneous series.

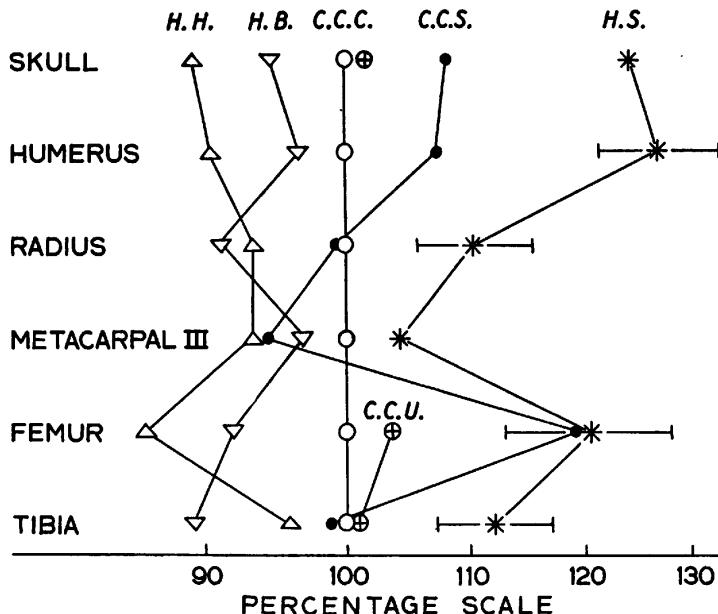


FIG. 9. Ratio diagram, comparing mean lengths of skull (prosthion to basion) and limb bones in samples of *Crocuta* and *Hyaena*. Abbreviations: C.c.c., *Crocuta c. crocuta*; C.c.s., *Crocuta c. spelaea*, Eggenburg; C.c.u., *Crocuta c. ultima*; H.b., *Hyaena brunnea*; H.h., *Hyaena hyaena*; H.s., *Hyaena sinensis*.

Crocuta eximia, as a representative of the *Percrocuta* division, is closer to *Crocuta* (*Crocuta*) than to *Hyaena*.

If there is really an intrapopulation allometry, it would mean that the relative difference between deciduous and permanent carnassials is pro-

TABLE 9
SKULL AND LIMB-BONE LENGTHS IN POPULATIONS OF *Crocuta* AND *Hyaena*

	<i>N</i>	<i>M</i>	σ	<i>V</i>	<i>O. R.^a</i>
<i>Crocuta crocuta crocuta</i>					
Prosthion to basion	9	228.3±3.8	11.5±2.7	5.02±1.19	206-248
Humerus	9	222.6±6.4	19.2±4.5	8.60±2.03	195-252
Radius	9	230.0±4.7	14.0±3.3	6.06±1.47	208-252
Third metacarpal	8	96.9±1.3	3.6±0.9	3.73±0.93	91-104
Femur	9	244.7±4.5	13.3±3.1	5.45±1.29	222-269
Tibia	9	195.1±4.5	13.6±3.2	6.95±1.64	180-219
<i>Crocuta crocuta spelaea</i>					
Prosthion to basion	5	249.6±5.7	12.7±4.0	5.09±1.61	232-271
Humerus	1	239	—	—	—
Radius	2	229	—	—	225-233
Third metacarpal	11	91.5±1.0	3.2±0.7	3.49±0.74	85-96
Femur	1	292	—	—	—
Tibia	1	193	—	—	—
<i>Crocuta crocuta ultima</i>					
Prosthion to basion	2	232	—	—	215-248
Femur	1	254	—	—	—
Tibia	1	197	—	—	—
<i>Hyaena hyaena</i>					
Prosthion to basion	7	200.0±3.1	8.2±2.2	4.10±1.09	178-214
Humerus	3	201.3	—	—	198-205
Radius	3	215.0	—	—	213-218
Third metacarpal	4	90.3±1.0	1.9±0.7	2.15±0.76	89-93
Femur	3	210.3	—	—	209-212
Tibia	3	187.0	—	—	181-191
<i>Hyaena brunnea</i>					
Prosthion to basion	16	217.1±1.2	4.6±0.8	2.14±0.38	207-226
Humerus	1	215	—	—	—
Radius	1	210	—	—	—
Third metacarpal	1	94	—	—	—
Femur	1	225	—	—	—
Tibia	1	174	—	—	—
<i>Hyaena sinensis</i>					
Prosthion to basion	3	278.2	—	—	265-300
Humerus	8	—	—	—	270-295
Radius	22	—	—	—	243-265
Third metacarpal	1	102	—	—	—
Femur	10	—	—	—	276-313
Tibia	26	—	—	—	209-228

^a Observed range.

gressively increased with increasing size without the intervention of special mutations. The same appears to be true for D_2 and D_3 compared with their permanent successors; the relationship is here essentially the same as for D_4 and M_1 .

LIMB PROPORTIONS

Figure 9 shows a comparison between the lengths of some limb segments and the prosthiion-basion lengths of the skull in some hyaenid samples. The data on the recent forms and on the cave hyena sample (from Eggenburg) are from Ehrenberg (1938-1940); those on *H. sinensis*, from Pei (1934a). For the lengths of humerus, radius, femur, and tibia, Pei gives only observed ranges of variation in a large series. The ranges are not great, and their midpoint will serve well enough for the present purpose. The length of the third metacarpal is measured from a specimen figured in Pei (1934a, pl. 21, fig. 8); the skull length is the mean of a low number of observations. The data on *C. c. ultima* are from Colbert and Hooijer (1953), with emendations (skull length), and from Boule and Teilhard (1928; limb bones). The statistics appear in table 9.

It is clear that the relative dimensions of the limbs are much more plastic characters than those of the teeth. Even the two fairly closely related species *H. hyaena* and *H. brunnea* differ strongly in proportions, and the differences between the two subspecies *C. c. crocuta* and *C. c. spelaea* are still greater. Figure 9, therefore, gives less information on the relationships between these forms than the previous study of the teeth. On the other hand it throws some light on the processes of adaptation within the different lines of evolution.

The difference between *C. c. crocuta* and *C. c. spelaea* consists of a relative shortening of the distal limb segments in the latter, apparently more strongly expressed in the hind limb (it should, however, be remembered that some of the cave hyena limb bones are represented by relatively scanty material). Whereas the proximal segments, humerus and femur, are much longer than their homologues in the recent form, radius and tibia are approximately of equal length in *C. c. spelaea* and *C. c. crocuta*, and the metacarpals (also the metatarsals, not represented in fig. 9) are actually shorter in the cave hyena. On the other hand, the sparse finds of *C. c. ultima* (a femur and a tibia from Ordos) agree well with the average dimensions in the recent form, as does the skull length of this subspecies. It is clear that the Ordos form, included in *C. c. spelaea* by Boule and Teilhard, does not belong there.

The differences between *H. hyaena* and *H. brunnea* are somewhat similar to those between *C. c. crocuta* and *C. c. spelaea*. *Hyaena brunnea*, again, has a longer humerus and femur, but a shorter radius and tibia; on the other hand, the metacarpals have not been shortened. In *H. sinensis* the trend has been analogous to that in the cave hyena even to the extent that the metacarpals have become rather short. The trend appears to be an adaptation to size increase and is seen in the "graviportal" type of many larger mammals, but this may not be the whole explanation. The marked shortening of the distal segments may have some connection with cave life. It is especially pronounced in the cave-living *C. c. spelaea* and *H. sinensis* and paralleled in the cave bear, *Ursus spelaeus* (see Ehrenberg, 1942). It is perhaps also suggestive that *C. c. ultima*, with its more orthodox limb proportions, seems to have been less exclusively cave-living. Pei records only one jaw from the Choukoutien *Sinanthropus* site, but thousands of specimens of *H. sinensis*.

In comparison with *C. c. crocuta*, *H. brunnea* and *H. sinensis* have relatively somewhat longer fore limbs and shorter hind limbs, whereas the trend in *C. c. spelaea* is the opposite.

TAXONOMY AND EVOLUTION

Crocuta crocuta ultima

I follow Colbert and Hooijer (1953) in regarding this form as a subspecies of the spotted hyena, *C. crocuta*, for the following reasons: (1) it can be shown that *C. c. spelaea*, which differs from the recent form more than *C. c. ultima*, probably was on a cline with the African population; (2) interjacent finds indicate continuity between the eastern and western populations; (3) such widely spread species of larger carnivores are common in our day (e.g., brown bear, wolf, lynx, striped hyena) and have evidently existed in earlier times (e.g., *Crocuta eximia* and *Ictitherium hipparium* of the Pontian). Four types of *Crocuta crocuta* appear to be well enough differentiated to merit subspecific recognition for the moment.

Crocuta crocuta crocuta (Erxleben)

This is the recent form; it has been split into a very great number of named races or subspecies (some of them proposed as species), which I propose to abolish, for the time being at any rate. The decision is based on a study of about 170 recent skulls, which are accounted for in greater detail elsewhere. It is true that some local populations are well differentiated from one another, but they appear to be connected by gradual

transitions without clear indication of stepped-up gradients. The end products of such spatial differentiation might, taken by themselves, merit subspecific recognition. Thus the South African form, *C. crocuta capensis* (Desmarest), averages considerably larger than the equatorial type. If we adhere to the 90 per cent rule formulated by Mayr *et al.* (1953), even this form has at best a very doubtful claim on subspecific recognition, and there is no clear indication of a boundary zone with a stepped-up gradient. (For further discussion of a somewhat analogous case and for an outline of the methods by which the problem should be studied, see Kurtén, 1955).

Some late Pleistocene fossils from the Middle East (e.g., Ksar 'Akil) apparently belong to this subspecies, but they show transitional characters between it and *C. c. spelaea*. The sparse finds from Süssenborn (Soergel, 1936) cannot now be shown to differ from the living subspecies, but may turn out to do so when more material is found.

Crocuta crocuta spelaea (Goldfuss)

The European cave hyena is very distinct from the nominate subspecies, partly on account of its large modal size (though the ranges overlap distally) and partly because of its aberrant limb proportions. The forms differ in many other characters, and the anatomical evidence (see Ehrenberg, 1938–1940) actually suggests full specific separation. On the other hand, there is evidence that this European population was continuous with southern, typical representatives of the nominate subspecies. The extent of this transitional zone is unknown. At any rate the typical cave hyena formed a large, well-differentiated population and may without hesitation be considered a distinct subspecies. It appears first in deposits of apparently Antepenultimate Glaciation (Mindel) age; the Forest Bed hyena from Corton Cliff (Newton, 1883) is already a typical cave hyena. *Hyaena intermedia* de Serres represents an artificially separated variant out of a normal population and is not a taxonomic unit.

The cave hyena probably evolved rapidly from the smaller initial migrant which would seem to be represented by the Süssenborn fossils.

Crocuta crocuta ultima (Matsumoto)

In this subspecies I include the late Pleistocene specimens from Ordos and Choei-tong-keou, which were determined by Boule and Teilhard as *C. c. spelaea*. Pei (1934a) unhesitatingly placed his late Pleistocene specimens from the Upper Cave at Choukoutien in *H. ultima*. It has been shown that the skeletal dimensions of this subspecies are close to those of *C. c. crocuta*, whereas the teeth are as large as those of the cave

hyena; this "Spezialisationskreuzung" suffices to distinguish the subspecies.

A Korean sample was described as a distinct subspecies, *Hyaena ultima dokantinensis*, by Tokunaga and Mori (1939; not seen).

Crocuta crocuta ultra Ewer

The Pleistocene form from the South African cave of Kromdraai was described by Broom (1939) under the name *C. spelaea capensis*. The name is a homonym of *C. crocuta capensis* (Desmarest) and is not available. Later, an excellent description of the type and new material was published by Ewer (1954b), who considered two species to be represented and gave the other the name *C. ultra*. The coexistence of two large hyaenid species of so closely similar facies is ecologically very improbable, and the variation does not appear to exceed that in other subspecies of *C. crocuta*. These forms are likely to represent an extinct subspecies probably, as Ewer points out, ancestral to the living population. The form is distinct from *C. c. crocuta* in a number of features, the relatively large M^1 being especially notable.

Recently, a number of forms with the *C. crocuta* facies were described from Swartkrans by Ewer (1955). She considers two species to be present, *C. crocuta* and *C. venustula*, but their many points of resemblance and the ecological argument would seem, again, to suggest that they represent a single population. This is the earliest certain record of *C. crocuta* in South Africa. The species has also been recorded from the Sterkfontein type site (Ewer, 1955), but the specimen appears to be of more recent date than the main fauna, judging from its state of fossilization and the character of the matrix in which it is embedded. Dietrich (1942) mentions *C. crocuta* from the Villafranchian Serengeti deposits, but the determination is based on fragmentary material which does not include the carnassials and cannot be accepted as evidence. As to the ages of the South African faunas, the fauna of Kromdraai is generally considered to be post-Villafranchian, whereas Ewer places Swartkrans in the late Villafranchian. The presence of *C. crocuta* may be of some importance for a determination of age, and I return to it below.

In addition to these subspecies, there is some evidence that others may have existed. The late Pleistocene Karnul Caves of India have yielded a *C. crocuta*, described by Rao under the name *C. pilgrimina* (*fide* Brongersma, 1937). The cast of a lower carnassial in the British Museum (Natural History) indicates a form of the size of a small *C. c. crocuta*; the talonid is very small; there is a small metaconid. If these characters are normal for the population, it may merit subspecific recog-

nition. The record goes far to prove continuity between the populations of the west and the east.

The descent of *C. crocuta* has been much debated. To me it appears most probable that *C. sivalensis* from the Pinjor Zone of the Siwaliks represents the immediate ancestor. This species is very close to the spotted hyena, and the characters in which they differ are more primitive in the Siwaliks form.

Crocuta sivalensis (Falconer and Cautley)

Matthew (1929) and Colbert (1935) have suggested that *H. felina* Bose and *H. colvini* Lydekker are identical with *C. sivalensis*, an opinion in which I concur. The variation in size between these forms is similar to that in other homogeneous populations (see table 5), and the variation in skull width, stressed by Pilgrim, is matched in *C. c. crocuta*. M^1 is modally larger than in *C. crocuta* and is apparently invariably present; its variation in size is natural in a vestigial structure. P^1 is lacking in the type of *H. felina*. In view of the perfect similarity between this form and the others the loss should probably be considered as an individual abnormality. I have seen a specimen of *H. brunnea* lacking P_2 . The absence of P^1 in B. M. No. 37138 is doubtful.

The situation has been confused by the incorrect assignment to *C. sivalensis* of an immature lower jaw of a large *Hyaena* (G.S.I. No. D102; see Pilgrim, 1932, p. 136). This specimen, which agrees in most characters with *H. brevirostris*, has a large P_2 and a short M_1 . Little is seen of the mandible teeth in the type of *C. sivalensis*, but P_2 can be made out well enough even on the British Museum cast to show that it is small and brachydont, with a well-marked posterior cusp, as in *C. crocuta*, *C. "felina,"* and *C. "colvini."* In the jaw, which is discussed further in the section on *H. sinensis*, this tooth is large, hypsodont, and has a reduced posterior cusp.

The most striking character of *C. sivalensis* is the long talonid on M_1 . This character is far outside the observed and theoretical ranges of variation in any known subspecies of *C. crocuta*. The presence of a large M^1 and a long talonid on M_1 , and the similarity to *C. crocuta* in other characters, strongly suggest that this species is the ancestor of the spotted hyena. Its stratigraphic position in a zone correlated with the later Villafranchian, and therefore earlier than any certain finds of the true *C. crocuta*, agrees with this interpretation. Furthermore, no other known Villafranchian form is at all likely to be ancestral to *C. crocuta*.

The following brief diagnoses are suggested for these forms:

SUBGENUS *CROCUTA* (*CROCUTA*) KAUP

Medium-sized to large Hyaenidae with elongate carnassials, reduced premolars, and relatively small canines; M^1 small or absent; P^4 with very long metastyle, reduced parastyle, and strong protocone extending obliquely forward; P^3 hypodont, with a small posterior cusp formed by the cingulum; P^2 and P_2 brachydont, with marked posterior cusps; M_1 with medium to very short talonid, long blade, and metaconid absent or vestigial. Only two species are known:

Crocuta (Crocuta) sivalensis (Falconer and Cautley)

A *Crocuta (Crocuta)* of medium size; M^1 present, modally larger than in *C. crocuta*; M_1 with vestigial metaconid and relatively long talonid.

Crocuta (Crocuta) crocuta (Erxleben)

A *Crocuta (Crocuta)* of medium to large size; M^1 small or absent; M_1 with very short talonid. At least four subspecies are known:

Crocuta (Crocuta) crocuta crocuta (Erxleben)

A Crocuta crocuta of medium size; M_1 generally without metaconid.

Crocuta (Crocuta) crocuta spelaea (Goldfuss)

A large *Crocuta crocuta*; M_1 frequently with metaconid; distal limb segments much shortened.

Crocuta (Crocuta) crocuta ultima (Matsumoto)

A Crocuta crocuta slightly larger than the nominate subspecies, and with similar limb proportions, but with dentition as heavy as that of *Crocuta crocuta spelaea*; M_1 frequently with metaconid; P^3 more hypodont than in other subspecies.

Crocuta (Crocuta) crocuta ultra Ewer

A Crocuta crocuta somewhat larger than the nominate subspecies, with M^1 modally larger than in other subspecies.

Hyaena sinensis

The *Hyaena* populations represented in the ratio diagram (fig. 6) fall into three groups: (1) *H. hyaena* alone; (2) *H. brunnea* and *H. perrieri*; and (3) the very large forms, *H. brevirostris*, *H. sinensis*, and *H. blythognatha* from the Pleistocene, and the Pliocene *H. salonicae*.

The relationships between the living *H. brunnea* and the Villafranchian *H. perrieri* are obscure, though probably much closer than has generally been supposed, but there can hardly be any doubt that they

form two quite distinct species. Though appearing much earlier in time, *H. perrieri* is more specialized than the recent form, e.g., in the almost complete loss of the metaconid in M_1 . That the two forms are descended from a common ancestor fairly late in the Pliocene seems, however, probable.

Hyaena perrieri was described by Croizet and Jobert from Mt. Perrier. Later, several specimens from other European localities were placed in this species. Boule (1893) identified *H. perrieri* with *H. topaciensis* Weithofer from Val d'Arno; he also thought it not unlikely that *H. brevirostris* Aymard from Sainzelles and *H. robusta* Weithofer from Val d'Arno represent large races of the same species. Viret (1954) agreed and, moreover, showed that *H. arvernensis* Croizet and Jobert from Mt. Perrier is identical with *H. perrieri*. The type of *H. arvernensis* has a small metaconid in M_1 , absent in *H. perrieri*, and for this reason Pilgrim (1931) placed the former in *Hyaena* and the latter in *Crocuta*. As is shown above, this character cannot be relied upon.

All these supposed species are from the Villafranchian of Europe, but *H. brevirostris* is also known from post-Villafranchian deposits. The species was based on a gigantic skull with associated mandible from Sainzelles; the type has been carefully redescribed by Boule (1893). Specimens of *H. brevirostris* were further identified by Soergel (1936) from Süßenborn, and in collections from the Forest Bed of Norfolk I have seen a number of fragmentary remains of a gigantic hyena which apparently represent the same species.

In size the type of *H. brevirostris* differs significantly from the normal *H. perrieri*. A joint analysis of the samples from Mt. Perrier and Saint-Vallier gives a mean length for M_1 of 25.23 ± 0.50 mm. (eight specimens), and a standard range of 20.6–29.8. The length of the lower carnassial from Sainzelles is about 30 mm., and the odds for its belonging to a similar population are less than one in 50. For the upper carnassial, the data are more decisive: the mean length in *H. perrieri* is 35.24 ± 0.61 mm. (seven specimens) and the standard range 30.0–40.4, whereas the Sainzelles specimen measures no less than 44.5 mm. Here the corresponding odds are far less than one to a thousand, and the type of *H. brevirostris* certainly represents a population differing strongly in average size from *H. perrieri*.

The means for *H. robusta* from Val d'Arno are given as 28.7 and 42.6 mm., respectively, by Soergel. The form is identical with *H. brevirostris*. The difference in size is trifling, and the only differentiating character might be the apparent presence of only one talonid cusp in the "robusta" M_1 (B. M. No. M4478), whereas *H. brevirostris* has two. A similar

variation is, however, found in the Javan *H. bathygnatha*.

The temporal relations between *H. perrieri* and *H. brevirostris* are not satisfactorily settled. Both (as represented by *H. "topariensis"* and *H. "robusta"*) are reported from Val d'Arno, but whether this means that they were perfectly contemporary or not cannot be decided at the moment. Yet this is of prime importance. The dimensions of the Val d'Arno specimens certainly fall into two distinct groups. Weithofer (1889) gives the lengths 40, 40, 41.5, and 42 mm. for four upper carnassials of *H. robusta*, and 34 mm. for one specimen of *H. topariensis*. Another specimen of *H. perrieri* (B. M. No. M469, labeled *H. striata*) from Val d'Arno measures 31.0 mm. This series does not represent a single homogeneous population. The coefficient of variation for the combined sample would be 10.8, a value so very much higher than values for P^4 in homogeneous samples (see table 6) as to indicate virtually certain heterogeneity. The sample should clearly be split into the two groups 31–34 mm. and 40–42 mm., representing two distinct populations.

If these populations were perfectly contemporary, they certainly represent two separate species, for, as is well known, two subspecies of the same mammalian species cannot exist in the same area at the same time, without merging. It might still be shown that the Val d'Arno fossils represent a chronocline within the Villafranchian series, but this cannot be proved at present, and the proper course is to keep *H. perrieri* and *H. brevirostris* separate.

There existed a third species of *Hyaena* in Europe during the Pleistocene. This was the living *H. hyaena*, represented by a relatively large subspecies, which seems to have been particularly frequent in the Iberian Peninsula during the later Pleistocene. The type was described in 1839 as *H. monspessulana* by de Christol and as *H. prisca* by de Serres, from Lunel-Viel, where it is associated with *C. c. spelaea* ("intermedia"). The name *H. prisca* is more often used, but Harlé (1910) accords priority to *H. monspessulana*. A specimen from Kreuznach was described as *H. matschiei* by Geib (1915), but distinguished on insufficient grounds (deviations in indices of no statistical value), and it is identical with *Hyaena hyaena monspessulana*. As seen from the ratio diagram (fig. 10), the form was somewhat larger than the living striped hyena, but the relative dimensions of the teeth were identical.

Some other finds from the European Pleistocene are of a somewhat uncertain status. Here may be mentioned *H. mosbachensis* Geib from the Mosbach sands (Geib, 1915; von Reichenau, 1906). The horizon is apparently the end of the Antepenultimate Interglacial. This form seems to be closely similar to *H. "arvernensis"* (= *H. perrieri*), but was con-

sidered distinct from that species by Geib (1915). The differences have no statistical significance. The metaconid, which is present, has shifted farther back than in the Villafranchian form, but probably little weight should be given to the variation in that vestigial element. *Hyaena mosbachensis* may possibly be classed as a straggler of *H. perrieri*.

When the Chinese and Javanese forms are compared with the European ones (figs. 6, 10) they are seen to be closer to *H. brevirostris* than to any other species. The mean dimensions of the three samples are almost identical. The question is whether these Eastern forms are likely to represent segments within a far-flung and essentially continuous population, including their European ally, and I believe this should be answered in the affirmative. There is no valid evidence for a specific separa-

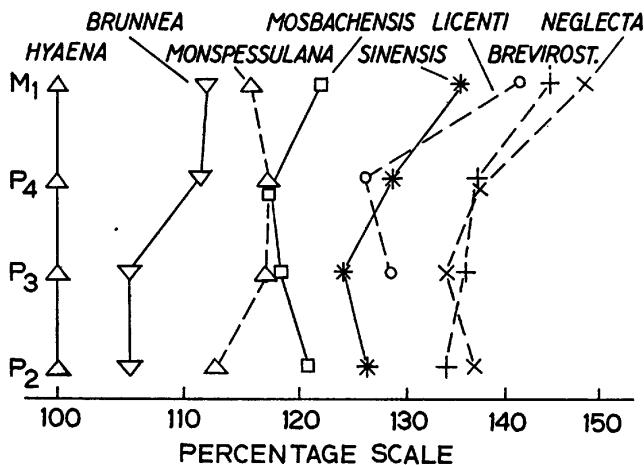


FIG. 10. Ratio diagram, comparing lengths of lower tooth crowns in single specimens and samples of *Hyaena*, as labeled. Dashed lines indicate single specimens.

tion between the eastern forms and the European population. Not only the dimensions but also the morphology is identical. The only differences are found in the development of the talonid in M₁. It is somewhat more reduced, modally, in *H. bathygnatha*, but similar differences distinguish the subspecies of *Crocuta crocuta*. Moreover, the talonid is unicuspis in *H. sinensis* and bicuspid in *H. licenti*, but both conditions occur in *H. brevirostris* and *H. bathygnatha*, and these differences are best accounted for as results of temporal and geographic subspeciation. The conclusion is strengthened by the analogy with *Crocuta crocuta* and with many recent carnivore species.

In this case also we have corroborative evidence from India. As noted

above, an immature jaw of a very large *Hyaena* (G.S.I. No. D102; cast, B. M. No. 1549) was referred by Lydekker (1884) to *C. felina*, and by Pilgrim (1932) to *C. sivalensis*. The specimen comes from Jammu. An unfigured ramus (G.S.I. No. D263) from Basaulan, Siwalik Hills, is stated by Pilgrim (1932) to agree with G.S.I. No. D102. Figure 10 is an outline drawing, based on the British Museum cast, and permits comparison with *H. brevirostris sinensis* and *C. c. ultima*.

The dimensions of this specimen agree almost exactly with those of the type of *H. brevirostris* (fig. 10). The dentitions, similarly, are almost identical, with the exception of P_2 . This tooth is of the same length as in *H. brevirostris*, but its posterior cusp is more reduced, a feature that I have not seen matched in any other subspecies of *H. brevirostris*. The morphological difference appears to justify the erection of a new subspecies, and it is diagnosed below under the name *Hyaena brevirostris neglecta*. The talonid of M_1 in this specimen has a strong entoconid. Unfortunately the hypoconid part is damaged, on the cast at any rate, but the talonid may well have been bicuspid. The existence of this form in India indicates the presence of a continuous *H. brevirostris* population from Europe to China during the Villafranchian.

For the units of *Hyaena* discussed here, the following brief diagnoses are suggested:

GENUS HYAENA BRISSON

Medium-sized to very large Hyaenidae with short carnassials, large canines, and large second premolars; M^1 functional, tricuspid; P^4 with short metastyle, fairly strong parastyle, and well-developed protocone extending medially; P^3 less hypodont than in *Crocuta* (*Crocuta*), with posterior cusp intervening between main cusp and cingulum; M_1 broad, with relatively well-developed, tricuspid to unicuspid talonid, the entoconid forming the strongest or only cusp, and metaconid present or absent.

Hyaena perrieri Croizet and Jobert

A *Hyaena* of medium size; M_1 with bicuspid talonid about as large as in *Hyaena brunnea*; metaconid occasionally present.

Hyaena brevirostris Aymard

A *Hyaena* of very large size; M_1 with bicuspid to unicuspid talonid, as large as in *Hyaena brunnea* or smaller; metaconid very rarely present. Several subspecies:

Hyaena brevirostris brevirostris Aymard

M_1 with bicuspid or unicuspid talonid, relatively short; metaconid not present.

Hyaena brevirostris licenti Pei

M_1 with bicuspid talonid.

Hyaena brevirostris sinensis Owen

M_1 with unicuspid talonid, relatively long; metaconid occasionally present.

Hyaena brevirostris bathygnatha Dubois

M_1 with bicuspid or unicuspid talonid, relatively short.

Hyaena brevirostris neglecta, new subspecies

TYPE: G.S.I. No. D102, a subadult left lower jaw (figured by Lydekker, 1884, pl. 38, fig. 1, pl. 39, fig. 1; and in this paper, fig. 11).

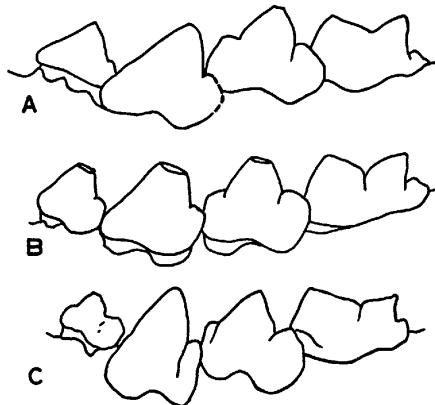


FIG. 11. Left lower cheek teeth of hyenas, external view. A. *Hyaena brevirostris neglecta*, new subspecies, cast of type, G.S.I. No. D102. B. *Hyaena brevirostris sinensis* Owen, redrawn after Zdansky. C. *Crocuta crocuta ultima* (Matsumoto), cast of A.M.N.H. No. 18730.

REFERRED SPECIMEN: Probably G.S.I. No. D263.

HORIZON AND LOCALITY: The Pinjor Zone, Siwaliks. The type locality is Jammu, Punjab.

DIAGNOSIS: P_2 with more reduced posterior cusp than in other subspecies.

Of these subspecies, *H. brevirostris bathygnatha* takes a position between *H. b. licenti* and *H. b. sinensis*, and might possibly be merged into one of these.

STRATIGRAPHIC SIGNIFICANCE

Figure 12 gives a tentative interpretation of the data in evolutionary and stratigraphic terms. The details of the replacement of *Hyaena brevirostris* by *Crocuta crocata* are clearest in the Choukoutien sequence, as described by Pei (1934a). In the strata below the *Sinanthropus* level, *H. brevirostris* occurs in great numbers; it is absent in the deposits immediately on top of the *Sinanthropus* level, where *Crocuta crocata* occurs. From this it would seem clear that this is a case of ecological replacement, and that it occurred at about the time of the Peking man settle-

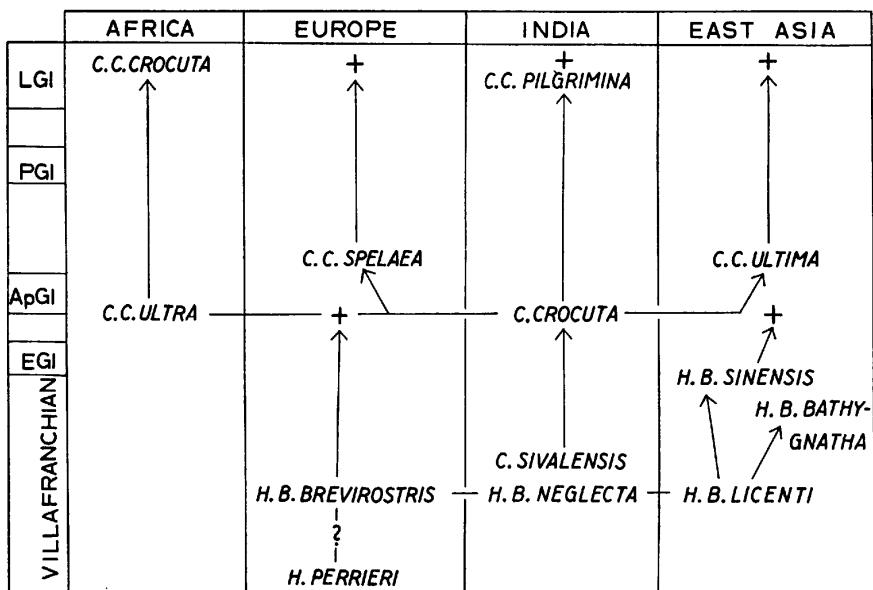


FIG. 12. Suggested phylogeny and stratigraphic relations of *Crocuta sivalensis*, subspecies of *C. crocata*, *Hyaena perrieri*, and subspecies of *H. brevirostris*, during the Pleistocene. Abbreviations: LGI, Late Glaciation; PGI, Penultimate Glaciation; ApGI, Antepenultimate Glaciation; EGI, Early Glaciation.

ment at Choukoutien. Otherwise, the faunas do not differ; witness the similarity between the Yenchingkou fauna, with *C. crocata*, and the Chinese faunas with *H. brevirostris*. It is thus clear that the *brevirostris-crocata* replacement permits a finer zonation of the stratigraphic sequence. That it concides with the time of Peking man adds to its interest.

From Europe we have evidence of the same transition at Süssenborn, where the details are less well known, and in the Forest Bed. The remains of *H. brevirostris* from the Forest Bed are all fragmentary and badly battered, but they are identifiable from the gigantic size of the

canines and rami and the large anterior premolars. Finds from Mundesley, Palling, and Bacton apparently represent this species. I have not seen the specimen from Bacton, which is in a private collection, but from a drawing shown to me by Mr. Ellis it appears likely to be *H. brevirostris*. On the other hand, finds from West Runton, Corton Cliff, and Palling represent *C. crocuta*. The good series of upper C-P⁴ from Corton Cliff described by Newton (1883) and kept in the Castle Museum indubitably belongs to the cave hyena. Thus the information on the occurrence of the two species in the Forest Bed is rather detailed.

There can be little doubt that the replacement at Süssenborn and in Norfolk was, geologically speaking, perfectly contemporaneous, and hence we may definitely state that Süssenborn is the equivalent of a certain level within the Forest Bed series. For Süssenborn the geological dating suggests the beginning of the first or second stage of the Antepenultimate (Mindel) Glaciation (Zeuner, 1953). I am aware that a later dating (Penultimate Glaciation) has been suggested by some authors (e.g., Papp and Thenius, 1949), but for several reasons this seems to me very unlikely. Thus we have a geologically fixed date for the *brevirostris-crocuta* replacement in Europe.

The question whether this European replacement can be correlated with the east Asian may, I think, be answered in the affirmative. The aspect would be different if, as has been thought, *C. c. spelaea* evolved in Europe from *H. brevirostris*, or if, for instance, the Chinese *C. c. ultima* represented the ancestor of the spotted hyena. In both cases the endemic form might be expected to occur earlier than the migrant. But as it seems that the species evolved in India from *C. sivalensis* and spread from there, the correlation appears to be justified. *Crocuta crocuta* seems to have been able to oust *H. brevirostris* throughout its range, and thus its spreading is likely to have covered a geologically negligible period. This gives us a date for *Sinanthropus* coinciding with the beginning or middle of the Antepenultimate Glaciation of Europe, or, with data from the radiation curve, on the order of 440,000–480,000 years ago (see Zeuner, 1953). This figure, if correct, is also the minimum age of the species *Crocuta crocuta*.

The closest contemporary of Peking man in Europe would be Heidelberg man; generally a somewhat higher age has been assigned to *Sinanthropus* (e.g., Zeuner, 1953). Heidelberg man is known from the Mosbachian of Mauer, from where we know no hyena. The Mosbach hyena, discussed above, may be *H. perrieri* but certainly not *C. crocuta*, and a greater age than that of Süssenborn is likely (an opinion also held, e.g., by Zeuner, though contested by Papp and Thenius). The age of the Mos-

bachian is likely to be the Antepenultimate (Günz-Mindel) Interglacial, slightly earlier than the *brevirostris-crocuta* replacement.

The Djetis Zone of Java, where *H. brevirostris bathygnatha* occurs, has been correlated with Choukoutien by Hooijer (e.g., 1951) and regarded as earlier by von Koenigswald (e.g., 1952). The present evidence is ambiguous, as *C. crocuta* apparently did not reach Java, but it may perhaps be suggestive that the Javanese *H. brevirostris* is intermediate in characters between the Villafranchian and post-Villafranchian subspecies in China. A late Villafranchian age is tentatively suggested.

Finally, the presence of *C. crocuta* at Swartkrans and in later African deposits appears to suggest that these faunas are not older than those of Choukoutien and the Antepenultimate Interglacial. However, it should be noted that *H. brevirostris* is not known from Africa, and thus it is possible that *C. crocuta* was able to spread thither at an earlier date. This possibility should be studied further, and the additional evidence of the remainder of the faunas considered, when the descriptions now in progress are completed.

EVOLUTIONARY SIGNIFICANCE

The main evolutionary conclusion to be drawn from the present study seems to me to be that it is possible to extend the modern "biological" species concept to paleontology, and that its application greatly clarifies a picture made unnecessarily incoherent by too much splitting. The basic question, in the comparison of two forms, is whether they are likely to have belonged to a continuously interbreeding population—not whether they agree or differ in certain morphological traits. Typology is necessary but fallacious if not interpreted in biological terms. That the biological species concept may also save us from indiscriminate lumping is exemplified by *H. perrieri* and *H. brevirostris* at Val d'Arno, the evidence in this case indicating that the species are distinct.

Apart from this, the new information on hyaenid phylogeny presents some features of interest. The early history of the genus *Hyaena* is rather obscure, as pointed out by Pilgrim (1931). We are now in a position to fill in some of its outlines from the beginning of the Pleistocene onward. The pre-Villafranchian sequence is largely unknown; *H. salonicae* might represent the ancestry of *H. brevirostris*, but the latter may also have branched from early representatives of *H. perrieri*. On the whole, the latter possibility appears more probable. The lines leading to the recent forms and to *H. perrieri* were probably differentiated in pre-Villafranchian times, but the center of distribution is unknown. Possibly it lay in Africa; an early Pleistocene subspecies of *H. brunnea* has been de-

scribed by Ewer (1955), and *H. namaquensis* Stromer may represent the ancestry of *H. hyaena*.

Of the Pleistocene species, *H. brevirostris* was initially very successful, spreading over a vast area and locally differentiating into many subspecies; some of these local populations persisted to the Antepenultimate Glaciation. The success of the genus *Hyaena* was later repeated within another line, that of *H. hyaena*. Its range is, at the present day, greater than that of any other living hyena, and in the late Pleistocene it was apparently still wider.

The center of evolution and distribution of the subgenus *Crocuta* (*Crocuta*) was, evidently, India south of the Himalayan range. Its pre-Villafranchian history is obscure, but it is quite likely to be wholly distinct from that of *Crocuta* (*Percrocuta*), and full generic separation may be found to be necessary. During the Pleistocene, the range of the evolving phylum was probably restricted to India until the Antepenultimate Glaciation of Europe, when it had evolved into the species *C. crocuta* which fanned out from the center and evolved into a number of subspecies in different parts of its range. Some of these subspecies apparently came close to full speciation. Towards the end of the Pleistocene most populations became extinct.

Thus, during the Pleistocene, a basically similar evolutionary pattern was repeated three times within different lineages: a species evolves in a limited area; it suddenly spreads over great areas, where it differentiates into incipient species; then it becomes extinct, or its range is diminished and it remains as a geographic relict. An analogous pattern is known to be common for higher categories. Its demonstration on the species level has been somewhat less common, perhaps because of the difficulties that arise in the delimitation of paleontological species.

The initial stage, the differentiation within a restricted area, is the most obscure point in most sequences, for obvious reasons. It is therefore particularly interesting that this phase appears to be recorded in one instance—that of *C. crocuta*. The center of distribution of *H. brevirostris* is unknown; that of *H. hyaena* is discussed above.

The rather dramatic metamorphosis from a local species into, as it were, an aggressively spreading form must result from evolutionary processes of great moment. These processes can only be guessed at, but it is probable that several factors combine and that their combination differs from case to case. Two main causes may be suggested: (1) the local form forces a geographic barrier and finds further spread unchecked; (2) the local form, adapted to local conditions and there keeping competing populations at bay, but inferior in different environments,

evolves characters giving it an advantage outside its original range, thus becoming able to spread and replace other species.¹ Both factors may have been of importance to *Crocuta crocuta*. The mountain range may have acted as a barrier, an important effect perhaps being the ecological dissimilarity between the environments on both sides of it. On the other hand, the evolutionary change from *C. sivalensis* to *C. crocuta*, which gives the latter a more progressive facies, suggests that the second factor may be involved, and apparently *C. crocuta* was able to replace *H. brevirostris* once it had become able to spread.

The differentiation into subspecies may occur during periods of migration, or afterward, or be initiated during the former and further developed in the latter phase. As far as the present data show, all three possibilities may have been realized. The first populations of *C. crocuta* in Europe and Africa were different from their descendants, and these latter evolved their peculiar characters *in situ*. On the other hand, the earliest *C. c. ultima* known from China appears already to possess the main characteristics of its late Pleistocene descendants.

Hyaena brevirostris is known only from differentiated populations, but the differentiation proceeded during the known Chinese sequence from *H. b. licenti* with its bicuspid talonid to *H. b. sinensis* in which the talonid is unicuspid.

The final event is extinction, and here, too, the causation is apparently always complex. The simplest situation is replacement by a better-adapted form, and this is probably the explanation of the extinction of *H. brevirostris*. The adaptive differences between recent *Hyaena* and *Crocuta* have been shown by Ewer (1954a) to be well reflected in the morphology and type of wear of the dentitions, and similar studies on *H. brevirostris* might be illuminating.

The extinction of *C. c. spelaea*, *C. c. ultima*, and *H. h. monspessulana*, on the other hand, was not due to competition; there has been no replacement. Perhaps the main factor was environmental change, wrought by climatic oscillation and the influence of man.

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¹ This latter alternative may also take the form of evolution in the environment, making that more suitable to the species in question; this is preadaptation.

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